

A revision of the superspecies *Hipparchia azorina* and of the *Hipparchia aristaeus* group (Nymphalidae : Satyrinae)

Alain OLIVIER* & John G. COUTSIS**

* Olivier, A : Luitenant Lippenslaan 43 B14, B-2140 Antwerpen, Belgium.

** Coutsis, J. : 4 Glykonos Street, GR-10675 Athens, Greece.

Summary

Arguments for the monophyly of *Hipparchia* (sensu Kudrna, 1977) and *Parahipparchia* are discussed : the latter taxon consists of one superspecies and two species groups. The *Hipparchia semele* group is characterized by two synapomorphies, including the (potential) presence of a sphragis at the end of the abdomen of the female when mated. The present study deals in particular with the other two entities, viz. superspecies *Hipparchia azorina* and the *Hipparchia aristaeus* group. Superspecies *H. azorina* is endemic to the Azores and consists of two semispecies, viz. *H. (azorina) azorina* and *H. (azorina) migueleensis* ; the former taxon consists of two subspecies, *azorina* (Pico and Faial) and *occidentalis* (Flores, Corvo, São Jorge and Terceira). *H. (azorina) migueleensis* is limited to the island of São Miguel. The nominal taxa *Hipparchia azorina cenjonatura* Bivar de Sousa, 1982, *Hipparchia azorina jorgense* Oehmig, 1983, *Hipparchia azorina barbara* Bivar de Sousa, 1985 and *Hipparchia azorina minima* Bivar de Sousa, 1985 are newly synonymized with *Hipparchia (azorina) azorina occidentalis* Bivar de Sousa, 1982 ; this arrangement differs from the previous ones mainly in that *occidentalis* appears to occur not only on the western island group, but also on part of the central island group. The *Hipparchia aristaeus* group is composed of four taxa, viz. *H. maderensis* (Madeira), *H. algerica* (Morocco, Algeria, Tunisia), *H. aristaeus* (Corsica, Sardinia, Elba, Giglio, Capraia) and *H. senthes* (Sicily, S. Italy, Albania, Former Yugoslav Republic of Macedonia, S. Bulgaria, Greece including the Aegean islands, western half of Turkey). The following taxa are newly synonymized with *Hipparchia senthes* (Fruhstorfer, 1908) : *Satyrus semele blachieri* Fruhstorfer, 1908, *Satyrus Semele* race *Siciliana* Oberthür, 1914, *Satyrus semele* L. f. *neapolitana* Stauder, 1921, *Hipparchia algerica vallettai* de Latrin, 1952, *Hipparchia algerica algerica vallettai* Valletta, 1972 and *Hipparchia ballettoi* Kudrna, 1984. Lectotypes are designated for *Satyrus Semele* race *Siciliana* Oberthür, 1914, *Satyrus semele* L. f. *neapolitana* Stauder, 1921 and *Satyrus semele* L. f. *blachierioides* Stauder, 1921. The latter taxon appears to be identical with *Hipparchia semele* (Linnaeus, 1758) and the synonymy established by Kudrna (1977) is thus confirmed. Each taxon is

described in detail and a comprehensive treatment of its distribution and bionomics is also included, as well as its taxonomic history including discussions on some nomenclatural problems. A list of characters that could be useful for the construction of a cladogram of *Parahipparchia* is presented: sixteen characters are retained and a series of characters previously listed by Balletto *et al.* (1990) is critically reviewed. The monophyly of the superspecies *H. azorina* is well supported; conversely, not a single synapomorphy has been detected for the *H. aristaeus* group, that could thus very well be a paraphyletic assemblage, either with or without the inclusion of the superspecies *H. azorina*. Priorities for further study are formulated: on one hand a comparative morphological study of all taxa (including early stages and adults) of *Parahipparchia* and *Hipparchia s. str.*, on the other hand a comprehensive study of molecular and allozyme data as an independent test of the phylogeny based on the morphological data set, as well as a means of estimating the possible divergence time of these taxa.

Zusammenfassung

Argumente für die Monophylie von *Hipparchia* (sensu Kudrna, 1977) und *Parahipparchia*, die eine Superspezies und zwei Artengruppen umfaßt, werden diskutiert. Die *Hipparchia semele* Artengruppe ist durch zwei Synapomorphien gekennzeichnet, darunter die Ausbildung einer Sphragis am Abdomenende von verpaarten Weibchen. Die vorliegende Arbeit widmet sich besonders den zwei anderen Gruppen, der Superspezies *Hipparchia azorina* und der *Hipparchia aristaeus* Artengruppe. Die Superspezies *H. azorina* ist endemisch für die Azoren und umfaßt zwei Semispezies, *H. (azorina) azorina* und *H. (azorina) miguelensis*. *H. azorina* enthält zwei Unterarten, *azorina* (Pico und Faial) und *occidentalis* (Flores, Corvo, São Jorge und Terceira). *H. (azorina) miguelensis* ist auf die Insel São Miguel beschränkt. Die nominellen Taxa *Hipparchia azorina cenjonatura* Bivar de Sousa, 1982, *Hipparchia azorina jorgense* Oehmig, 1983, *Hipparchia azorina barbara* Bivar de Sousa, 1985 und *Hipparchia azorina minima* Bivar de Sousa, 1985 werden mit *Hipparchia (azorina) azorina occidentalis* Bivar de Sousa, 1982 synonymisiert. Diese Anordnung unterscheidet sich von bisherigen Klassifikationen darin, daß *occidentalis* nunmehr nicht nur auf der westlichen sondern auch der zentralen Inselgruppe vorkommt. Die *Hipparchia aristaeus* Artengruppe besteht aus vier Arten, *H. maderensis* (Madeira), *H. algerica* (Marokko, Algerien, Tunesien), *H. aristaeus* (Korsika, Sardinien, Elba, Giglio, Capraia) und *H. senthes* (Sizilien, Süd-Italien, Albanien, ehem. jugoslawische Republik Mazedonien, Süd-Bulgarien, Griechenland inklusive der aegäischen Inseln, westliche Türkei). Die folgenden Taxa werden mit *H. senthes* (Fruhstorfer, 1908) synonymisiert: *Satyrus semele blachieri* Fruhstorfer, 1908, *Satyrus Semele* race *Siciliana* Oberthür, 1914, *Satyrus semele* L. f. *neapolitana* Stauder, 1921, *Hipparchia algerica vallettai* de Lattin, 1952, *Hipparchia algerica vallettai* Valletta, 1972 und *Hipparchia ballettoi* Kudrna, 1984. Lectotypen werden für *Satyrus Semele* race *Siciliana* Oberthür, 1914, *Satyrus semele* L. f. *neapolitana* Stauder, 1921

und *Satyrus semele* L. f. *blachieroides* Stauder, 1921, festgelegt. Das letztgenannte Taxon ist *Hipparchia semele* (Linnaeus, 1758) sehr ähnlich und die von Kudrna (1977) festgestellte Synonymie wird bestätigt. Alle behandelten Taxa werden detailliert beschrieben und ihre Verbreitung, Phänologie und bisherige taxonomische Stellung ausführlich dargestellt, sowie einige nomenklatorische Probleme diskutiert. Merkmale, die für die Erstellung eines Kladogramms von *Parahipparchia* nützlich/verwendbar sein können, werden aufgelistet, wobei 16 Merkmale vorgeschlagen werden und einige von Balletto *et al.* (1990) kritisch überprüft werden. Die Monophylie der Superspezies *H. azorina* ist gut begründet, aber für die *H. aristaeus* Artengruppe konnte keine einzige Synapomorphie ermittelt werden. Es könnte sich hierbei um ein Paraphylum handeln, entweder mit oder ohne Einschluss der Superspezies *H. azorina*. Für künftige Untersuchungen werden folgende Prioritäten formuliert: Einerseits vergleichend morphologische Untersuchungen sowohl an Imagines wie Präimaginalstadien aller Taxa von *Parahipparchia* und *Hipparchia* s. str., andererseits umfassende molekulare und enzymelektrophoretische Studien, mit Hilfe deren Daten ein unabhängiger Test der auf morphologischer Grundlage gewonnenen phylogenetischen Hypothesen möglich ist und die außerdem Anhaltspunkte zur Abschätzung des evolutionären Alters dieser Taxa bieten.

Résumé

Le caractère monophylétique de *Hipparchia* (sensu Kudrna, 1977) et de *Parahipparchia* est discuté : ce dernier taxon est composé d'une super-espèce et de deux groupes d'espèces. Le groupe de *Hipparchia semele* peut être identifié à l'aide de deux synapomorphies, incluant la présence (potentielle) d'un sphragis à l'extrémité de l'abdomen de la femelle fécondée. La présente étude traite en particulier des deux autres entités, à savoir la super-espèce *Hipparchia azorina* et le groupe d'espèces de *Hipparchia aristaeus*. La super-espèce *H. azorina* est endémique aux Açores et consiste de deux semi-espèces, à savoir *H. (azorina) azorina* et *H. (azorina) miguelensis* ; le premier taxon inclue deux sous-espèces, *azorina* (Pico et Faial) et *occidentalis* (Flores, Corvo, São Jorge et Terceira). *H. (azorina) miguelensis* est limité à l'île de São Miguel. Les taxons nominaux *Hipparchia azorina cenjonatura* Bivar de Sousa, 1982, *Hipparchia azorina jorgense* Oehmig, 1983, *Hipparchia azorina barbara* Bivar de Sousa, 1985 et *Hipparchia azorina minima* Bivar de Sousa, 1985 sont nouvellement établis comme synonymes de *Hipparchia (azorina) azorina occidentalis* Bivar de Sousa, 1982 ; cet arrangement diffère des précédents principalement par le fait qu'il est démontré que *occidentalis* n'est pas limité au groupe d'îles occidental, mais occupe également une partie du groupe d'îles central. Le groupe de *Hipparchia aristaeus* se compose de quatre taxons, à savoir *H. maderensis* (Madère), *H. algerica* (Maroc, Algérie, Tunisie), *H. aristaeus* (Corse, Sardaigne, Elbe, Giglio, Capraia) et *H. senthes* (Sicile, Italie méridionale, Albanie, l'ancienne république yougoslave de Macédoine, Bulgarie méridionale, Grèce incluant les îles égéennes, moitié occidentale de la Turquie).

Les taxons suivants sont nouvellement établis comme synonymes de *Hipparchia senthes* (Fruhstorfer, 1908) : *Satyrus semele blachieri* Fruhstorfer, 1908, *Satyrus Semele* race *Siciliana* Oberthür, 1914, *Satyrus semele* L. f. *neapolitana* Stauder, 1921, *Hipparchia algerica vallettai* de Lattin, 1952, *Hipparchia algerica vallettai* Valletta, 1972 et *Hipparchia ballettoi* Kudrna, 1984. Des lectotypes sont désignés pour *Satyrus Semele* race *Siciliana* Oberthür, 1914, *Satyrus semele* L. f. *neapolitana* Stauder, 1921 et *Satyrus semele* L. f. *blachierioides* Stauder, 1921. Ce dernier taxon étant identique à *Hipparchia semele* (Linnaeus, 1758), la synonymie établie par Kudrna (1977) est confirmée. Chaque taxon est décrit en détail et sa distribution géographique et bionomie est également discutée de manière approfondie, ainsi que son histoire taxinomique, incluant des discussions sur quelques problèmes de nomenclature. Une liste de caractères qui pourraient être utilisables lors de la construction d'un cladogramme de *Parahipparchia* est présentée : seize caractères sont retenus et une série de caractères précédemment énumérés par Balletto *et al.* (1990) est discutée de manière critique. Le caractère monophylétique de la super-espèce *H. azorina* est bien corroboré ; en revanche, aucune synapomorphie propre au groupe de *Hipparchia aristaeus* n'a pu être détectée. Ainsi, ce dernier ensemble pourrait-il bien être paraphylétique, avec ou sans l'inclusion de la super-espèce *H. azorina*. Des priorités pour l'étude ultérieure sont formulées : d'une part une étude morphologique comparative de tous les taxons (incluant les premiers états et les adultes) faisant partie de *Parahipparchia* et de *Hipparchia s. str.*, d'autre part une étude complète de données moléculaires et enzymatiques (allozymes) comme test indépendant de la phylogénie basée sur l'ensemble des données morphologiques, ainsi que comme moyen d'estimation de l'âge de divergence possible de ces taxons.

1. Introduction

1.1. Delimitation of the genus *Hipparchia*

The genus *Hipparchia* (sensu Kudrna, 1977) consists of five currently recognized subgenera, i. e. *Hipparchia* Fabricius, 1807, *Parahipparchia* Kudrna, 1977, *Neohipparchia* de Lesse, 1951, *Euhipparchia* Kudrna, 1977 and *Pseudotergumia* Agenjo, 1948. Some of these subgenera have been considered by several authors as either distinct genera when compared to *Hipparchia s. str.* (e. g. Higgins, 1975 ; Koçak, 1981–1983) or species groups (“Artengruppen”) that should not be named formally (e. g. Hesselbarth, van Oorschot & Wagener, 1995) : this is, however, merely a semantic issue. What matters is that the supraspecific taxon one recognizes be a monophyletic unit. In order to do so, one should identify at least one synapomorphy that characterizes it. The decision of ranking at any hierarchical level is largely dependent on the scope of one's study.

The monophyly of *Hipparchia s. l.* (sensu Kudrna, 1977) has recently been questioned, though it is, according to García-Barros & Martín (1991), supported by 7 synapomorphies, 5 of which are adult morphological characters. At least one of these, however — the presence of a Jullien organ — is irrelevant, as such a structure has been found as well in *Pseudochazara* (see Hesselbarth, van Oorschot & Wagener, 1995 : 939, figs. 66 & 67), in other genera of the subtribe Satyriti (sensu Harvey, 1991) and even in more distantly related satyrine taxa (Dampf, 1908 : 77, fig. 2 ; De Prins & Olivier, unpublished data). A structure, that was named Jullien organ as well, has also been found in *Maniola* (see e. g. Wüest-Jullien, 1980 ; Thomson, 1991) and it could therefore represent a homoplasy, as noted by García-Barros & Martín (1991 : 408).

1.2. Delimitation of the subgenus *Parahipparchia*

The subgenus *Parahipparchia* is presumably monophyletic : beside a recognizably distinct general wing pattern, the species composing it share at least one probable synapomorphy, i. e. androconial scales of the eomorphic/palaeomorphic type (Kudrna, 1977, 1984 ; Bivar de Sousa, 1982a, 1985b ; Oehmig, 1983), except for one single species, *Hipparchia (Parahipparchia) mersina* (Staudinger, 1871) (Kudrna, 1977 ; Olivier & De Prins, 1989). Its sister group is likely to be subgenus *Hipparchia s. str.* (see García-Barros & Martín, 1991), of which all known species have a neomorphic type of androconium (Kudrna, 1977). Such also seems to be the case with the three other subgenera of *Hipparchia* (sensu Kudrna, 1977), as well as in all remaining genera of the Satyriti investigated in this respect, when androconia are present at all (*Brintesia*, *Arethusana*, *Chazara*, *Pseudochazara*, *Satyrus*, *Berberia*, cf. Le Cerf, 1914 ; de Lesse, 1954 ; Higgins, 1975 ; Brown, 1976 ; Kudrna, 1977 ; Gross, 1978 ; De Prins & van der Poorten, 1981 ; Sakai, 1981 ; Nekrutenko, 1990 ; García-Barros & Martín, 1991 ; Skolka, 1997 ; Wakeham-Dawson, 1997), except *Karanasa*, where all conditions from the eomorphic/palaeomorphic to the neomorphic type have been found (Avinoff & Sweadner, 1951 ; Sakai, 1981). There is, however, no further evidence in support of a direct sister group relationship between *Parahipparchia* and *Karanasa*. It is worth mentioning that outside the Satyriti the various types of androconial scale have been found in other subtribes of the tribe Satyrini sensu Harvey (1991), i. e. in the genera *Erebia* (see Warren, 1936) and *Coenonympha* (see Davenport, 1941), while only the neomorphic type is known in the Manioliti (de Freina & Aussem, 1987 ; Thomson, 1987 ; Samodurov *et al.*, 1995, 1996a, 1996b).

1.3. Subdivisions within *Parahipparchia*

In the present study, we recognize one superspecies and two species groups within *Parahipparchia*. The arrangement adopted for the superspecies and the first group is totally new and is based on the results of the present revision (see below). The second group is based on our own preliminary analysis of data presented in Kudrna (1977, 1984, 1986, 1996), Coutsis (1984), Balletto *et al.* (1990) and Cesaroni *et al.* (1994), supplemented with our own unpublished results. This leads to the following new classification of subgenus *Parahipparchia* :

— Superspecies *Hipparchia azorina*

Hipparchia (azorina) azorina (Strecker, 1899), **comb. n., stat. n.**

Hipparchia (azorina) azorina azorina (Strecker, 1899), **comb. n., stat. n.**

Hipparchia (azorina) azorina occidentalis Bivar de Sousa, 1982, **comb. n., stat. n.**

Hipparchia (azorina) miguelensis (Le Cerf, 1935), **comb. n., stat. n.**

— *Hipparchia aristaeus* group

Hipparchia maderensis (Baker, 1891)

Hipparchia algerica (Oberthür, 1876)

Hipparchia aristaeus (Bonelli, 1826)

Hipparchia senthes (Fruhstorfer, 1908)

— *Hipparchia semele* group

Hipparchia semele (Linnaeus, 1758)

Hipparchia sbordonii Kudrna, 1984

Hipparchia leighebi Kudrna, 1976

Hipparchia cretica (Rebel, 1916)

Hipparchia mersina (Staudinger, 1871)

Hipparchia volgensis (Mazochin-Porshnjakov, 1952)

Hipparchia turcmenica Heydemann, 1942

Hipparchia christenseni Kudrna, 1977

Hipparchia pellucida (Stauder, 1924)

Hipparchia pellucida pellucida (Stauder, 1924)

Hipparchia pellucida cypriensis (Holik, 1949)

The last-named group will not be revised in the present paper. Therefore, we will limit ourselves to the following comments.

The monophyly of the *H. semele* group is supported by at least two synapomorphies : the (potential) presence of a sphragis at the end of the abdomen of the female when mated and the average length of the dorsal lamella exceeding 0.7 mm (see section 7 for a further

discussion). The sphragis is invariably present in *H. cretica*, *H. sbordonii*, *H. leighebi*, *H. mersina*, *H. volgensis* and *H. christenseni*. In *H. semele*, it is always present among material from Spain, southern France and southern Italy (Sicily, Calabria, Basilicata), while in material from Central Europe (e. g. Belgium) it is usually absent or barely visible. In *H. pellucida*, a sphragis is always present among specimens from Kípros (Cyprus) and most Turkish populations, while it was found in only one single female from the Greek island of Lésvos, but in none from the Greek island of Ikaría. In *H. turcmenica* we haven't noticed it, but we saw only two females. As far as we know, the phylogenetically most closely related species in which a sphragis has been recorded is the Australian satyrine *Heteronympha penelope* Waterhouse, 1937 (tribe Satyrini, subtribe Hypocystiti), while such a structure is known as well in *Acraea* (Nymphalidae), but especially in the Papilionidae (Orr, 1995).

We consider the unique condition of the androconium in *H. mersina* as an autapomorphy (character state reversal) of this species. Such seems to be the most parsimonious solution, otherwise one should have to assume that it is the sister species of the whole remainder of *Parahipparchia*, and hence that a series of other characters originated at least twice in this subgenus or became lost again in both superspecies *H. azorina* and the *H. aristaeus* group. A further discussion of these and other topics is beyond the scope of the present study. See, however, sections 7 and 8 for a preliminary phylogenetic analysis.

2. On the colour plates

Initially we intended to revise only the taxa of the *H. aristaeus* group from the Italian mainland, Sicily, the Balkans and Turkey. For that purpose, in 1995, all relevant type material was borrowed from several museums for illustration and lectotype designations. Specimens have since been sent back with a red label referring to the present publication, mentioning the number of the colour plate and of the figure on which each individual type specimen was to be shown. All this material was referred to either plate 1 or 2.

In the meantime, we considered it not only appropriate but also necessary to broaden the scope of our study to the other taxa of the *H. aristaeus* group, as well as those from the Azores: this has resulted in two more colour plates, that bear the numbers 3 and 4 in the present article. This choice of numbering, although in reverse of the order of treatment of each nominal taxon in the present paper, was made in order not to contradict the references on the labels of the type specimens we are dealing with in this study.

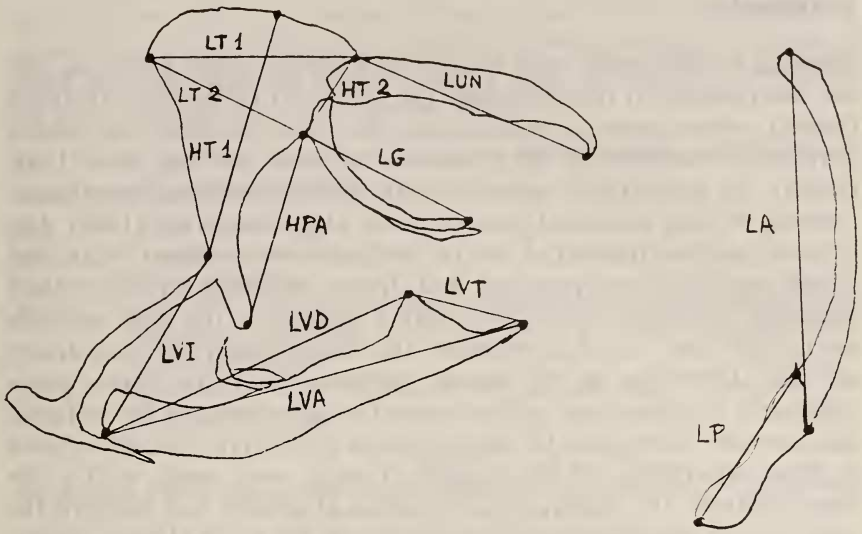


Fig. 1. Male genitalia : measurements used for table 2.

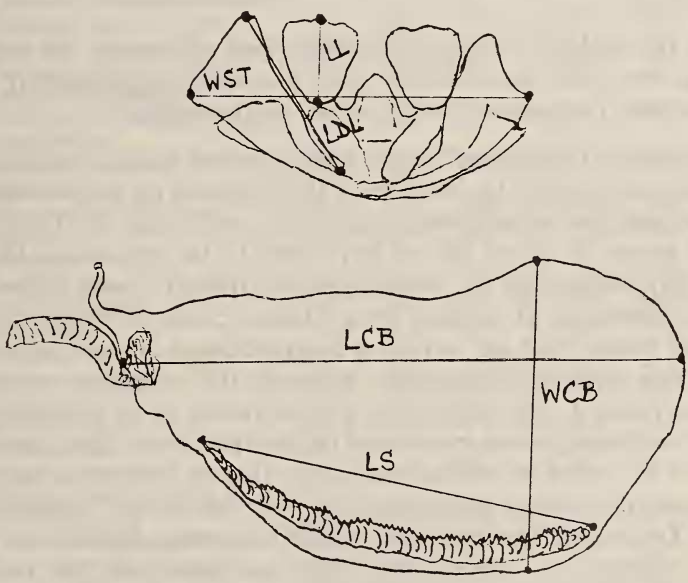


Fig. 2. Female genitalia : measurements used for table 3.

3. Methods

Material is listed under each recognised nominal taxon. Forewing size has been measured from the base (at the costa) to the apex (without fringes): when larger samples for an area were available, we limited ourselves to samples of 25 specimens for each sex (see table 1 for results). No quantitative measurements of wing markings were made. Naming of wing veins and spaces follows Higgins & Riley (1984). The genitalia and androconia of several specimens were studied. Male and female genitalia were prepared and drawn according to the method described in Coutsis (1984: 161–162). Drawings of the male genitalia are in side view: in a few instances, the Jullien organ has been drawn as well. Drawings of the female genitalia show the entire bursa copulatrix (sterigma and corpus bursae) in side view and the sterigma also dorsally. Sometimes the ductus bursae with cervix bursae is shown in detail separately. All the original drawings were made with a 25 \times magnification. The naming of the various structures and parts of the male and female genitalia follows Olivier & De Prins (1989). Various morphometric measurements were carried out, as shown on text figs. 1 & 2 and proportions of some of these structures in relation to each other were calculated (tables 2 & 3). Single androconial scales were photographed in black and white (phase contrast) with a 400 \times magnification.

Data on the biology, ecology, phenology and chorology are derived from our own field observations when available, supplemented by a comprehensive treatment of the literature on the subject.

In our heading "Comments" under each nominal taxon, considerable effort has been put into the analysis of the literature on matters dealing with taxonomy and nomenclature, especially concerning the *Hipparchia aristaeus* group. In doing so, we have tried to be exhaustive, though we are fully aware that we certainly have "missed" some references, especially about e.g. *H. senthes* from Turkey, Sicily or Malta. Nevertheless, we believe that our survey is comprehensive enough to include all important relevant information. Although this treatment may seem somewhat prolix to the reader, we are convinced of its usefulness, as so many conflicting views, errors and misinterpretations have been laid down over the years by various authors, either as a result of different species concepts, wrong applications of the rules of the International Code of Zoological Nomenclature (ICZN), or mere ignorance of the primary sources, i. e. the existing type specimens and the original descriptions. For each nominal taxon we will list the complete synonymy as well as the existing type material and its current depository

when known. We have checked all the original descriptions ourselves, as well as the type specimens when this proved necessary : several of these are illustrated on plates 1 and 2 and we designate lectotypes for three nominal taxa in the present study.

The following abbreviations of collectors and (museum) collections are used throughout this publication :

- AO = Alain Olivier
- JGC = John G. Coutsis
- NG = Nikos Ghavalas
- VLCA = Vlaamse Lepidoptera Collectie Antwerpen (composed of the former individual collections of W. De Prins, J. Dils, A. Olivier & D. van der Poorten)
- ZMA = Instituut voor Systematiek en Populatiebiologie, Zoölogisch Museum, Amsterdam

Table 1

Superspecies *Hipparchia azorina* and the *Hipparchia aristaeus* group : right forewing size (from base to apex) in mm

Taxon/Area of origin	Males				Females			
	Min.	Max.	Mean	n	Min.	Max.	Mean	n
<i>H. (azorina) azorina azorina</i>								
Portugal, Azores, Pico	19.7	21.8	21.1	9	22.3	25.0	23.8	3
Portugal, Azores, Faial	19.3	21.3	20.4	10	22.5	25.4	23.7	5
<i>H. (azorina) azorina occidentalis</i>								
Portugal, Azores, Flores	18.4	20.0	19.2	6	19.9	22.7	21.3	3
Portugal, Azores, São Jorge	20.0	22.0	21.2	4	22.6	23.5	23.1	2
Portugal, Azores, Terceira	18.6	20.8	19.7	8	20.0	23.5	21.9	4
<i>H. (azorina) miguelensis</i>								
Portugal, Azores, São Miguel	20.7	22.8	21.7	21	24.0	25.7	24.6	7
<i>H. maderensis</i>								
Portugal, Madeira	20.8	26.0	24.0	25	24.2	29.3	26.7	25
<i>H. algerica</i>								
Morocco, Middle Atlas	22.6	26.1	24.7	25	25.9	30.2	27.8	25
Algeria	23.4	26.6	24.9	7	24.9	29.8	27.7	10
<i>H. aristaeus</i>								
Italy, Sardinia	22.3	25.5	24.3	25	25.0	29.6	26.9	25
France, Corsica	22.7	25.6	24.6	25	24.5	28.5	26.2	14
Italy, Elba	24.3	26.2	24.9	4	26.9	28.6	27.6	6
<i>H. senthes</i>								
Turkey, Antalya	23.6	27.8	25.7	25	22.4	29.6	27.7	25
Greece, Sámos	24.2	27.8	26.6	23	27.7	31.4	29.5	8
Greece, Ikaría	24.5	30.0	27.0	16	26.4	31.0	28.7	25
Greece, Híos	24.1	27.7	26.0	25	26.0	29.9	27.7	25
Greece, Kiklâdes, Páros	26.1	30.8	28.8	15	28.6	32.1	30.5	9
Greece, Central Greece & Pelopónissos	24.5	28.3	27.2	23	25.6	31.6	29.8	15
Greece, Northeastern Greece	23.9	27.9	25.9	14	25.5	29.7	28.2	12
Italy, Sicily, Le Madonie	26.0	29.4	27.6	25	26.4	33.2	30.7	25
Italy, Calabria, La Sila	23.9	28.0	26.4	17	22.5	34.4	29.5	25
Italy, Campania, Monte Faito	24.9	28.4	26.7	25	24.8	31.3	29.0	25
Italy, Campania, Ísola d' Íschia	24.5	30.4	27.5	25	28.4	31.9	30.3	7

Table 2
Morphometric measurements (in mm) taken on male genitalia and various proportions (see fig. 1)

Prep. No.	Origin	LUN	LTI	LT2	LG	HT1	HT2	HPA	LVI	LVA	LVD	LVT	LA	LP	LA+LP	LUN/LTI	LUN/LG	LUN+LTI/LVA	LUN+LTI/LA+LP
2543	Portugal, Azores, Pico	0.86	1.00	0.88	0.67	0.92	0.38	0.77	1.08	1.81	1.33	0.58	1.35	0.73	2.08	0.86	1.28	1.03	0.89
2814	Portugal, Azores, Pico	0.85	0.94	0.88	0.65	0.96	0.38	0.77	0.88	1.73	1.35	0.50	1.56	0.69	2.25	0.90	1.31	1.03	0.79
2815	Portugal, Azores, Pico	0.86	0.92	0.85	0.67	1.00	0.35	0.81	0.88	1.67	1.36	0.48	1.46	0.79	2.25	0.93	1.28	1.07	0.79
2542	Portugal, Azores, Faial	0.85	0.98	0.90	0.65	0.88	0.38	0.75	0.98	1.69	1.33	0.52	1.54	0.71	2.25	0.87	1.31	1.08	0.81
2810	Portugal, Azores, Faial	0.86	0.96	0.83	0.67	1.02	0.40	0.77	0.85	1.62	1.33	0.46	1.46	0.69	2.15	0.90	1.28	1.12	0.85
2811	Portugal, Azores, Faial	0.83	0.88	0.81	0.65	0.87	0.38	0.73	0.85	1.71	1.31	0.58	1.58	0.69	2.27	0.94	1.28	1.00	0.75
2795	Portugal, Azores, Flores	0.90	0.88	0.79	0.67	0.96	0.38	0.77	0.81	1.63	1.29	0.46	1.38	0.69	2.07	1.02	1.34	1.09	0.86
2796	Portugal, Azores, Flores	0.92	1.02	0.96	0.67	0.92	0.38	0.79	0.88	1.77	1.33	0.56	1.46	0.73	2.19	0.90	1.37	1.10	0.89
2797	Portugal, Azores, Flores	0.92	0.98	0.90	0.63	0.92	0.38	0.75	0.88	1.73	1.28	0.56	1.37	0.67	2.04	0.94	1.46	1.10	0.93
2805	Portugal, Azores, São Jorge	0.96	1.02	0.92	0.65	0.96	0.42	0.79	0.87	1.85	1.46	0.60	1.60	0.75	2.35	0.94	1.48	1.07	0.84
2806	Portugal, Azores, São Jorge	0.85	0.92	0.81	0.69	0.90	0.40	0.75	0.92	1.63	1.31	0.48	1.38	0.67	2.05	0.92	1.23	1.09	0.86
2807	Portugal, Azores, São Jorge	0.90	0.87	0.83	0.67	0.94	0.38	0.81	0.96	1.67	1.38	0.48	1.46	0.77	2.23	1.03	1.34	1.06	0.79
2544	Portugal, Azores, Terceira	0.77	0.87	0.81	0.62	0.90	0.35	0.75	0.83	1.48	1.19	0.42	1.35	0.73	2.08	0.89	1.24	1.11	0.79
2801	Portugal, Azores, Terceira	0.85	0.88	0.87	0.60	0.90	0.37	0.77	0.87	1.67	1.31	0.52	1.44	0.62	2.06	0.97	1.42	1.04	0.84
2802	Portugal, Azores, Terceira	0.85	0.87	0.77	0.60	0.87	0.37	0.75	0.83	1.58	1.27	0.50	1.29	0.63	1.92	0.98	1.42	1.09	0.90
2545	Portugal, Azores, São Miguel	1.11	1.00	0.88	0.77	1.06	0.40	0.85	0.96	1.77	1.42	0.50	1.60	0.71	2.31	1.11	1.44	1.19	0.91
2818	Portugal, Azores, São Miguel	1.08	1.00	0.94	0.73	1.06	0.40	0.88	1.02	1.77	1.40	0.54	1.42	0.77	2.19	1.08	1.48	1.18	0.95
2819	Portugal, Azores, São Miguel	1.04	0.94	0.90	0.63	0.96	0.38	0.85	1.00	1.69	1.38	0.42	1.35	0.67	2.02	1.11	1.65	1.17	0.98
2820	Portugal, Azores, São Miguel	1.06	0.96	0.90	0.71	1.00	0.42	0.83	1.02	1.77	1.40	0.50	1.42	0.71	2.13	1.10	1.49	1.14	0.95

Prep. No.	Origin	LUN	LT1	LT2	LG	HT1	HT2	HPA	LVI	LVA	LVD	LVT	LA	LP	LA+ LP	LUN/ LT1	LUN/ LG	LUN+ LT1/ LVA	LUN+ LT1/ LA+LP
2532	Portugal, Madeira	1.15	1.10	1.04	0.75	1.10	0.44	0.94	1.08	2.12	1.69	0.54	1.83	0.98	2.81	1.05	1.53	1.06	0.80
2533	Portugal, Madeira	1.19	1.08	1.00	0.80	1.15	0.40	1.02	1.00	2.17	1.73	0.62	1.85	0.94	2.79	1.10	1.49	1.05	0.81
2534	Portugal, Madeira	1.19	1.04	0.96	0.85	1.17	0.40	1.08	1.12	2.12	1.67	0.56	2.00	0.96	2.96	1.14	1.40	1.05	0.75
2535	Portugal, Madeira	1.23	1.17	1.10	0.81	1.21	0.40	1.13	1.17	2.21	1.85	0.60	1.96	1.04	3.00	1.05	1.52	1.09	0.80
2536	Portugal, Madeira	1.27	1.15	1.08	0.79	1.19	0.42	1.04	1.10	2.10	1.71	0.60	1.79	0.94	2.73	1.10	1.61	1.15	0.89
2411	Morocco, Middle Atlas	1.25	1.13	1.06	0.73	1.19	0.48	0.98	1.15	2.17	1.69	0.60	1.75	0.87	2.62	1.11	1.71	1.10	0.91
2412	Morocco, Middle Atlas	1.21	1.06	1.00	0.77	1.31	0.44	1.08	1.00	2.10	1.65	0.56	1.98	1.00	2.98	1.14	1.57	1.08	0.76
2524	Morocco, Middle Atlas	1.21	1.12	0.98	0.79	1.21	0.46	1.02	1.17	2.08	1.69	0.58	1.83	0.85	2.68	1.08	1.53	1.12	0.87
2525	Morocco, Middle Atlas	1.17	0.98	0.90	0.73	1.19	0.42	1.00	1.08	2.02	1.62	0.62	1.79	0.87	2.66	1.19	1.60	1.06	0.81
2526	Morocco, Middle Atlas	1.23	1.15	1.02	0.75	1.23	0.46	1.02	1.06	2.06	1.65	0.54	1.94	0.98	2.92	1.07	1.64	1.16	0.82
2271	Italy, Sardinia	1.29	1.02	0.98	0.77	1.19	0.40	1.10	1.19	2.15	1.77	0.58	1.86	1.06	2.92	1.26	1.68	1.07	0.79
2272	Italy, Sardinia	1.31	1.10	1.06	0.75	1.25	0.44	1.08	1.08	2.28	1.88	0.58	1.79	0.88	2.67	1.19	1.75	1.06	0.90
2273	Italy, Sardinia	1.19	1.19	1.08	0.73	1.17	0.46	0.98	1.15	2.19	1.77	0.60	1.75	0.87	2.62	1.00	1.63	1.09	0.91
2274	Italy, Sardinia	1.23	1.08	1.02	0.73	1.12	0.38	1.04	1.15	2.23	1.79	0.58	1.64	0.94	2.58	1.14	1.68	1.04	0.90
2294	Italy, Sardinia	1.33	1.10	0.96	0.79	1.23	0.48	1.10	1.31	2.38	1.92	0.62	2.06	1.04	3.10	1.21	1.68	1.02	0.78
2520	Italy, Sardinia	1.33	1.13	1.00	0.81	1.19	0.44	1.10	1.38	2.31	1.88	0.56	1.83	0.94	2.77	1.18	1.64	1.06	0.89
2521	Italy, Sardinia	1.27	1.06	1.02	0.73	1.23	0.46	1.04	1.10	2.15	1.75	0.54	1.69	0.96	2.65	1.20	1.74	1.08	0.88
2275	France, Corsica	1.23	1.06	0.94	0.73	1.15	0.44	1.00	1.15	2.06	1.69	0.52	1.71	0.94	2.65	1.16	1.68	1.11	0.86
2270	Italy, Elba	1.27	1.12	1.04	0.73	1.23	0.44	1.07	1.15	2.27	1.79	0.62	1.69	1.10	2.79	1.13	1.74	1.05	0.86
2276	Italy, Sicily	1.54	1.35	1.13	1.15	1.40	0.56	1.15	1.35	2.50	1.94	0.71	2.27	1.02	3.29	1.14	1.34	1.16	0.88

Prep. No.	Origin	LUN	LTI	LT2	LG	HT1	HT2	HPA	LVI	LVA	LVD	LVT	LA	LP	LA+LP	LUN/LTI/LG	LUN+LTI/LVA	LUN+LTI/LVA+LP	
2277	Italy, Sicily	1.54	1.27	1.13	1.10	1.48	0.54	1.27	1.27	2.56	2.08	0.63	2.21	1.08	3.29	1.21	1.40	1.10	0.85
2278	Italy, Sicily	1.46	1.21	1.17	0.98	1.52	0.54	1.13	1.37	2.42	2.00	0.62	2.13	0.98	3.11	1.21	1.49	1.10	0.86
2292	Italy, Sicily	1.46	1.19	1.08	1.08	1.46	0.50	1.21	1.15	2.40	1.90	0.63	2.04	1.12	3.16	1.23	1.35	1.10	0.84
2299	Italy, Sicily	1.48	1.21	1.10	1.06	1.52	0.52	1.21	1.27	2.58	2.00	0.73	2.15	1.12	3.27	1.22	1.40	1.04	0.82
2386	Italy, Sicily	1.44	1.31	1.15	1.02	1.52	0.54	1.19	1.19	2.37	1.92	0.63	2.23	1.21	3.44	1.10	1.41	1.16	0.80
2387	Italy, Sicily	1.46	1.25	1.17	1.00	1.62	0.60	1.29	1.33	2.52	1.96	0.69	2.21	1.08	3.29	1.17	1.46	1.08	0.82
2344	Italy, Calabria, Aspromonte (RE)	1.54	1.21	1.06	1.10	1.54	0.54	1.19	1.27	2.60	2.02	0.71	2.10	1.13	3.23	1.27	1.40	1.06	0.85
2345	Italy, Calabria, Aspromonte (RE)	1.60	1.29	1.12	1.17	1.46	0.54	1.17	1.15	2.50	1.94	0.71	2.13	1.08	3.21	1.24	1.37	1.16	0.90
2358	Italy, Calabria, La Sila (CS)	1.54	1.23	1.02	1.23	1.54	0.56	1.15	1.27	2.33	1.98	0.56	2.17	1.25	3.42	1.25	1.25	1.19	0.81
2359	Italy, Calabria, La Sila (CS)	1.63	1.33	1.10	1.35	1.65	0.58	1.31	1.27	2.69	2.10	0.75	2.27	1.27	3.54	1.23	1.21	1.10	0.84
2362	Italy, Calabria, La Sila (CS)	1.67	1.23	1.04	1.31	1.54	0.56	1.29	1.27	2.52	1.96	0.69	2.29	1.29	3.58	1.36	1.27	1.15	0.81
2363	Italy, Calabria, La Sila (CS)	1.58	1.27	1.06	1.29	1.60	0.60	1.21	1.25	2.46	1.96	0.67	2.23	1.21	3.44	1.24	1.22	1.16	0.83
2364	Italy, Calabria, La Sila (CS)	1.67	1.31	1.13	1.25	1.58	0.58	1.27	1.17	2.63	2.06	0.73	2.29	1.23	3.52	1.27	1.34	1.13	0.85
2365	Italy, Calabria, La Sila (CS)	1.44	1.15	1.06	1.13	1.58	0.56	1.13	0.98	2.38	1.96	0.52	2.15	1.06	3.21	1.25	1.27	1.09	0.81
2285	Italy, Campania, Monte Faito (NA)	1.58	1.37	1.10	1.31	1.60	0.56	1.31	1.15	2.63	2.04	0.73	2.21	1.12	3.33	1.15	1.21	1.12	0.89
2293	Italy, Campania, Monte Faito (NA)	1.50	1.23	1.06	1.21	1.54	0.58	1.29	1.25	2.52	2.04	0.65	2.31	1.08	3.39	1.22	1.24	1.08	0.81
2295	Italy, Campania, Monte Faito (NA)	1.56	1.23	1.04	1.27	1.52	0.54	1.23	1.08	2.60	2.04	0.71	2.19	1.13	3.32	1.27	1.23	1.07	0.84
2298	Italy, Campania, Monte Faito (NA)	1.50	1.37	1.15	1.29	1.71	0.52	1.35	1.19	2.52	2.00	0.65	2.08	1.13	3.21	1.09	1.16	1.14	0.89
2323	Italy, Campania, Monte Faito (NA)	1.67	1.27	1.08	1.29	1.65	0.50	1.31	1.17	2.62	2.08	0.73	2.40	1.37	3.77	1.31	1.29	1.12	0.78
2287	Italy, Campania, Isola di Capri (NA)	1.60	1.31	1.08	1.31	1.58	0.60	1.25	1.15	2.60	2.12	0.63	2.19	1.27	3.46	1.22	1.22	1.12	0.84

Prep. No.	Origin	LUN	LT1	LT2	LG	HT1	HT2	HPA	LVI	LVA	LVD	LVT	LA	LP	LA+LP	LUN/LG	LUN+LT1/LVA	LUN+LT1/LA+LP	
2286	Italy, Campania, Ísola d'Íschia (NA)	1.58	1.33	1.15	1.23	1.63	0.60	1.23	1.23	2.58	2.02	0.75	2.17	1.15	3.32	1.19	1.28	1.13	0.88
2291	Italy, Campania, Ísola d'Íschia (NA)	1.52	1.40	1.19	1.12	1.50	0.52	1.17	1.23	2.71	2.15	0.73	2.15	1.15	3.30	1.09	1.36	1.08	0.88
2503	Greece, Pelopónissos	1.63	1.23	1.08	1.12	1.46	0.54	1.13	1.21	2.60	2.06	0.67	2.23	1.06	3.29	1.33	1.46	1.10	0.87
2504	Greece, Pelopónissos	1.56	1.25	1.04	1.10	1.54	0.60	1.15	1.13	2.44	1.90	0.71	2.13	1.13	3.26	1.25	1.42	1.15	0.86
2505	Greece, Pelopónissos	1.62	1.19	1.04	1.17	1.50	0.56	1.29	1.19	2.63	2.04	0.73	2.29	1.12	3.41	1.36	1.38	1.07	0.82
2440	Greece, Pelopónissos	1.50	1.29	1.10	1.17	1.52	0.54	1.17	1.12	2.40	1.96	0.60	2.06	1.04	3.10	1.16	1.28	1.16	0.90
2506	Greece, Stereá Eliáda	1.54	1.27	1.02	1.13	1.38	0.56	1.21	1.17	2.56	2.00	0.73	2.23	1.00	3.23	1.21	1.36	1.10	0.87
2507	Greece, Stereá Eliáda	1.52	1.29	1.12	1.19	1.58	0.58	1.35	1.23	2.54	1.98	0.69	2.21	1.25	3.46	1.18	1.28	1.11	0.81
2508	Greece, Atíki	1.50	1.19	1.00	1.04	1.50	0.54	1.17	1.12	2.37	1.88	0.60	2.06	1.08	3.14	1.26	1.44	1.14	0.86
2439	Greece, Makedonia	1.54	1.21	1.06	1.19	1.60	0.52	1.25	1.02	2.38	1.87	0.69	2.06	1.08	3.14	1.27	1.29	1.16	0.88
2302	Greece, Kikládes, Siros	1.67	1.42	1.27	1.15	1.62	0.62	1.37	1.35	2.65	2.13	0.71	2.29	1.15	3.44	1.18	1.45	1.17	0.90
2441	Greece, Kikládes, Mílos	1.73	1.31	1.08	1.19	1.50	0.58	1.27	1.33	2.71	2.13	0.71	2.27	1.13	3.40	1.32	1.45	1.12	0.89
2509	Greece, Eastern Aegean islands, Ikaría	1.48	1.31	1.12	1.12	1.50	0.54	1.19	1.19	2.44	2.00	0.62	2.23	1.08	3.31	1.13	1.32	1.14	0.84
2510	Greece, Eastern Aegean islands, Ikaría	1.50	1.27	1.10	1.17	1.50	0.56	1.19	1.21	2.44	1.90	0.67	2.25	1.06	3.31	1.18	1.28	1.14	0.84
2511	Greece, Eastern Aegean islands, Ikaría	1.46	1.19	1.04	1.08	1.42	0.54	1.17	1.21	2.48	1.88	0.69	2.17	1.06	3.23	1.23	1.35	1.07	0.82
2410	Turkey, Muğla	1.38	1.15	0.98	1.04	1.42	0.50	1.08	1.02	2.23	1.77	0.58	2.08	1.02	3.10	1.20	1.33	1.13	0.82
2409	Turkey, Antalya	1.38	1.15	0.98	0.98	1.40	0.48	1.13	1.06	2.37	1.85	0.63	1.96	1.06	3.02	1.20	1.41	1.07	0.84
2408	Turkey, Konya	1.37	1.13	1.02	1.06	1.40	0.46	1.10	1.12	2.37	1.87	0.65	1.98	1.08	3.06	1.21	1.29	1.05	0.82

Table 3

Morphometric measurements (in mm) taken on female genitalia (see fig. 2)

Prep. No.	Origin	WST	LDL	LL	LCB	WCB	LS
2547	Portugal, Azores, Pico	1.88	0.92	0.35	2.02	1.35	1.04
2816	Portugal, Azores, Pico	1.65	0.88	0.35	1.71	1.10	1.10
2817	Portugal, Azores, Pico	1.83	0.88	0.38	1.90	0.88	0.96
2546	Portugal, Azores, Faial	1.96	0.81	0.42	1.96	1.04	1.00
2812	Portugal, Azores, Faial	1.87	1.15	0.44	2.19	1.23	1.15
2813	Portugal, Azores, Faial	1.65	0.92	0.35	1.90	1.27	1.17
2798	Portugal, Azores, Flores	1.60	0.96	0.37	2.10	1.35	1.08
2799	Portugal, Azores, Flores	1.58	0.88	0.37	1.71	1.13	0.80
2800	Portugal, Azores, Flores	1.62	0.87	0.37	1.71	1.21	1.12
2808	Portugal, Azores, São Jorge	1.67	0.87	0.37	2.12	1.37	1.25
2809	Portugal, Azores, São Jorge	1.83	0.90	0.37	2.33	1.27	1.27
2548	Portugal, Azores, Terceira	1.69	1.00	0.37	1.48	0.88	0.77
2803	Portugal, Azores, Terceira	1.56	1.00	0.37	1.90	1.21	0.96
2804	Portugal, Azores, Terceira	1.69	0.88	0.35	1.69	0.96	1.06
2821	Portugal, Azores, São Miguel	1.94	1.00	0.44	2.44	1.25	1.35
2822	Portugal, Azores, São Miguel	1.71	0.92	0.35	2.58	1.31	1.52
2823	Portugal, Azores, São Miguel	1.81	0.88	0.42	2.33	1.29	1.50
2537	Portugal, Madeira	2.08	1.25	0.56	3.92	1.77	2.88
2538	Portugal, Madeira	1.85	1.10	0.48	3.88	1.90	2.85
2539	Portugal, Madeira	1.90	1.19	0.48	3.85	1.88	2.62
2540	Portugal, Madeira	2.15	1.00	0.58	3.50	2.15	2.62
2541	Portugal, Madeira	1.88	0.88	0.56	3.85	1.77	3.06
2527	Morocco, Middle Atlas	1.77	1.06	0.52	2.96	1.13	2.42
2528	Morocco, Middle Atlas	1.67	0.96	0.48	3.58	1.60	2.65
2529	Morocco, Middle Atlas	1.92	1.02	0.46	3.19	1.81	2.35
2530	Morocco, Middle Atlas	1.79	0.98	0.52	3.38	1.87	2.52
2531	Morocco, Middle Atlas	1.60	1.08	0.46	3.52	1.83	2.27
2320	Italy, Sardinia	1.96	1.15	0.56	3.42	1.17	2.65
2321	Italy, Sardinia	1.92	1.23	0.54	3.65	1.42	2.69
2461	Italy, Sardinia	1.60	1.15	0.52	3.63	1.69	2.87
2462	Italy, Sardinia	1.83	1.13	0.56	3.90	1.71	2.96
2463	Italy, Sardinia	1.98	1.33	0.62	3.37	1.13	2.96

Prep. No.	Origin	WST	LDL	LL	LCB	WCB	LS
2522	Italy, Sardinia	1.69	1.25	0.54	3.65	1.85	2.69
2523	Italy, Sardinia	1.69	1.19	0.60	3.29	1.23	2.67
2464	France, Corsica	1.90	1.08	0.56	4.27	1.69	2.77
2465	Italy, Elba	1.90	1.12	0.50	3.75	1.98	2.96
2319	Italy, Sicily	1.94	1.27	0.48	4.56	2.21	3.19
2451	Italy, Sicily	2.00	1.29	0.62	4.23	1.79	3.17
2452	Italy, Sicily	2.00	1.19	0.62	4.48	1.83	3.38
2453	Italy, Sicily	2.02	1.10	0.58	4.67	2.23	3.40
2367	Italy, Calabria, La Sila (CS)	2.06	1.15	0.73	4.40	1.48	2.87
2368	Italy, Calabria, La Sila (CS)	1.92	1.17	0.69	4.10	1.54	3.23
2372	Italy, Calabria, La Sila (CS)	2.13	1.06	0.65	4.75	1.69	2.81
2373	Italy, Calabria, La Sila (CS)	2.00	1.33	0.79	3.58	1.62	2.60
2374	Italy, Calabria, La Sila (CS)	1.85	1.17	0.69	3.50	1.48	2.58
2379	Italy, Calabria, La Sila (CS)	2.23	1.25	0.67	4.10	1.83	2.88
2380	Italy, Calabria, La Sila (CS)	1.85	1.31	0.73	3.94	1.65	2.46
2381	Italy, Calabria, La Sila (CS)	2.27	1.35	0.75	3.77	1.56	2.73
2382	Italy, Calabria, La Sila (CS)	1.87	1.19	0.71	4.25	2.08	3.15
2383	Italy, Calabria, La Sila (CS)	1.92	1.04	0.58	3.98	1.44	2.79
2384	Italy, Calabria, La Sila (CS)	2.19	1.31	0.75	3.88	1.37	2.69
2824	Italy, Calabria, La Sila (CS)	2.37	1.31	0.73	3.67	1.50	2.88
2454	Italy, Campania, Monte Faito (NA)	1.85	1.12	0.58	3.44	1.17	2.88
2455	Italy, Campania, Monte Faito (NA)	2.13	1.31	0.65	3.33	1.90	2.69
2456	Italy, Campania, Monte Faito (NA)	2.10	1.10	0.54	4.54	2.50	3.27
2457	Italy, Campania, Monte Faito (NA)	2.02	1.08	0.63	3.50	1.12	2.85
2458	Italy, Campania, Monte Faito (NA)	2.04	1.23	0.71	4.00	1.96	2.90
2459	Italy, Campania, Ísola d'Íschia (NA)	2.02	1.42	0.75	3.50	1.29	3.02
2460	Italy, Campania, Ísola d'Íschia (NA)	2.02	1.10	0.73	3.77	1.44	3.06
2512	Greece, Pelopónissos	2.17	1.35	0.71	4.31	2.04	3.08
2517	Greece, Pelopónissos	2.00	1.23	0.71	3.63	1.88	2.75
2513	Greece, Stereá Eláda	1.92	1.23	0.67	3.77	1.87	2.65
2514	Greece, Stereá Eláda	2.04	1.04	0.60	3.71	1.85	2.46
2516	Greece, Stereá Eláda	2.00	1.21	0.69	4.38	1.87	2.67
2518	Greece, Eastern Aegean islands, Ikaría	2.19	1.25	0.63	3.85	1.44	3.06
2519	Greece, Eastern Aegean islands, Ikaría	1.85	1.02	0.56	3.33	1.17	2.42

4. Superspecies *Hipparchia azorina*

DESCRIPTION. Overall size less than any other *Parahipparchia* species. Ground-colour dark brown, wing markings on upperside much reduced to completely absent, especially in the males. Sex brand much reduced or even totally absent. Upperside forewing in females lighter brown-grey to creamy white in basal and discal area, due to thinner scaling in combination with lighter pigmentation. Male genitalia smaller than any other *Parahipparchia* species, both in overall size and (nearly always) in size of the different parts; uncus \leq tegumen (*azorina*) or $> 1.1 \times$ tegumen length (*miguelensis*); valve with well developed dorsal process; aedeagus dorsally with small spines in its distal half. Female genitalia sterigma not significantly smaller to equally sized to *maderensis*, *algirica* and *aristaeus*, but dorsal lamella and — on average — dorso-lateral lobe always smaller than any other *Parahipparchia* species; cervix bursae lightly sclerotized, corpus bursae distinctly smaller and signum distinctly shorter than in any other *Parahipparchia* species, except some *mersina* (cf. Olivier & De Prins, 1989).

DISTRIBUTION. Restricted to the Azores (Portugal), where it is known to occur on the islands of Flores, Corvo, São Jorge, Terceira, Faial, Pico and São Miguel.

COMMENTS. It was Le Cerf (1935 : 209) who discovered the presence of spines on the aedeagus in *azorina* from Pico and in *miguelensis*, highlighting its significance. Of all subsequent authors, only Bivar de Sousa (1982a) mentioned this character : we haven't seen any material from Corvo but we found it in all males dissected from the six other islands of the archipelago, while it has not been observed in any other *Hipparchia* s. l. Therefore, we consider it to be a synapomorphy of superspecies *H. azorina*. The superspecies concept, as defined by Mayr (1963), applies very well to the present case, i. e. "a monophyletic group of entirely or essentially allopatric species that are morphologically too different to be included in a single species (...) that reproductive isolation between them can be assumed". Oehmig (1983) already suggested use of this concept, recognizing three component species instead of two in the present study (see below).

Bernardi (1961) applied the superspecies concept to the *H. aristaeus* group with the inclusion of *azorina*. We have been unable to find any synapomorphy supporting the monophyly of the *aristaeus* group so far, either with or without *azorina*, and therefore we see no hard evidence for the existence of a superspecies *H. aristaeus* as viewed by Bernardi. For the same reason we cannot follow Leestmans (1968),

Higgins (1975) and Higgins & Hargreaves (1983) in considering *azorina* as a subspecies of *H. aristaeus*. There is even less support for considering *azorina* as a subspecies of *H. semele* (cf. Cockerell, 1923 ; Rebel, 1938, 1940a, 1940b ; Carthy, 1957).

4.1. *Hipparchia (azorina) azorina* (Strecker, 1899) comb. n., stat. n.

“*Satyrus Azorinus* n. sp.” Strecker, 1899. — Lepidoptera, Rhopaloceres and Heteroceres, Indigenous and Exotic. Supplement No. 2 : 3. Locus typicus restrictus : [Azores] Pico (Oehmig, 1983 : 139). Type material : holotype (by monotypy) ♂, Allyn Museum of Entomology, Sarasota, Florida, USA. For synonymy, see subspecies.

TYPE LOCALITY. Strecker (1899) reported his unique specimen as originating from the “Azores”, without further specification. It is so worn, that it is impossible to attribute it to any island population with any certainty, except that it definitely doesn’t come from São Miguel. Bivar de Sousa (1982a : 207) compared the original description of this taxon to a picture of the holotype and to some specimens from the island of Faial and concluded that it came from that island, the more as Faial was normally the island visited by ships en route between Europe and North America during the 19th Century. Oehmig (1983 : 139), however, having also examined pictures of that specimen (reproduced here on text fig. 3), not only concluded that it came from Pico, but formally proposed to restrict the type locality to this island. Therefore, Pico is to be considered as the type locality of the present species.

DESCRIPTION. Mean size in both sexes less than *H. (azorina) miguelensis*, varying to some extent among different islands : smallest on Corvo, Flores and Terceira, largest on Pico, São Jorge and Faial. Wing markings even more reduced than in *miguelensis* ; creamy yellow (or orange) submarginal patches upperside hindwing (usually present to various degrees in s2–s5(6) in all other *Parahipparchia* taxa) invariably absent. Basal and discal area upperside forewing lighter grey to creamy white, as in female, in few males of *H. (azorina) azorina azorina* and in all examined males of *H. (azorina) azorina occidentalis*. Upperside hindwing spot in s2 usually absent. Underside hindwing discal line bending abruptly distally in s4–s5 and often ending in a point, bordered distally by moderately broad whitish postdiscal band that is always well-expressed. Male genitalia smaller than in *miguelensis*, uncus \leq tegumen. Female genitalia, mid-dorsal process as a rule wide at base, usually more or less triangular or rounded ; corpus bursae smaller than in *miguelensis* (and *mersina*) ; signum shorter than in *miguelensis* and in most *mersina*.

A



B

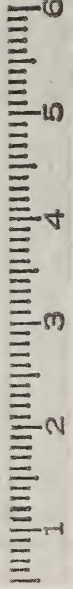


Fig. 3. Holotype of *Satyrus Azorinus* Strecker, 1899 [= *Hipparchia (azorina) azorina azorina* (Strecker, 1899)]. A. Upperside. B. Underside.

DISTRIBUTION. As superspecies *H. azorina* (vide supra), but absent from São Miguel.

BIONOMICS. The biotope consists of natural grasslands, usually at altitudes from 500 m up to 2000 m on Pico, with various shrubs and herbs including a. o. *Calluna vulgaris* (L.), *Erica azorea* Hochst. ex Seub., *Rubus* spp. and *Potentilla* spp., both last ones visited by the imagines (for further details see Walker, 1931 ; Le Cerf, 1935 ; Carthy, 1957 ; Marsden & Wright, 1971 ; Oehmig, 1983 ; Meyer, 1991, 1993 ; Fuchs, 1993). Larval host-plant *Festuca jubata* Lowe (Poaceae) (Oehmig, 1983 ; according to Fuchs, 1993, *F. petraea* Bracen). Univoltine : adults from June (Rebel, 1940b) to October (Walker, 1931), in a protracted brood. Early stages : described in detail by Oehmig (1983) from material from both Faial and Flores.

GEOGRAPHIC VARIATION. There is some (minor) inter-island variation in external and structural characters, as well as in morphology of the early stages. This has led to the formal description of a subspecies for each single inhabited island (Le Cerf, 1935 ; Esaki, 1936 ; Bivar de Sousa, 1982a, 1982b, 1985b ; Oehmig, 1983). Last-named author raised the Flores population to species rank, as opposed to those from the central island group (Pico, Faial and São Jorge) : in this he was followed by Kudrna (1986, 1996), Balletto *et al.* (1990), Vieira & Pintureau (1991), Meyer (1991, 1993), Balletto (1995) and Tolman & Lewington (1997). We recognize only one species with two subspecies for both central and western island groups, with a different distribution than was assumed until now (see below).

4.1.1. *Hipparchia (azorina) azorina azorina* (Strecker, 1899) comb. n., stat. n.

“*Satyris Azorinus* n. sp.” Strecker, 1899. — Lepidoptera, Rhopaloceres and Heteroceres, Indigenous and Exotic. Supplement No. 2 : 3. Locus typicus restrictus : [Azores] Pico (Oehmig, 1983 : 139). Type material : holotype (by monotypy) ♂, Allyn Museum of Entomology, Sarasota, Florida, USA.

“*Satyris azorinus* Strecker, ssp. *piccensis*, nova” Le Cerf, 1935. — *Bull. Soc. ent. Fr.* 40 : 206–208, Pl. V, figs. 6–10. Locus typicus : Azores, Pico. Type material : syntypes 2 ♂, 1 ♀, in Muséum National d’Histoire Naturelle, Paris. — Junior subjective synonym of *Satyris Azorinus* Strecker, 1899 (Rebel, 1940b : 16 ; Kudrna, 1977 : 97).

“*Oeneis ohshimai* sp. nov.” Esaki, 1936. — *Annotnes. zool. jap.* 15 : 483–485. Locus typicus : Azores, Faial. Type material : holotype

♂, paratypes 2 ♂, 4 ♀, in Entomological Laboratory, Kyūshū Imperial University, Fukuoka. — Junior subjective synonym of *Satyris Azorinus* Strecker, 1899 (Rebel, 1940b : 16 ; Kudrna, 1977 : 97).

“*Oeneis okohimae*” Rebel, 1940b. — *Soc. Scient. Fenn., Comm. Biol.* VIII.1 : 16. — Subsequent misspelling of the name *ohshimai* Esaki, 1936.

“*Hipparchia azorensis*” Bernardi, 1961. — *Colloques int. Cent. natn. Rech. scient.* 94 : 186. — Subsequent misspelling of the name *Azorinus* Strecker, 1899.

ILLUSTRATIONS. Plate 3, figs. 1–2 & 4–5. Plate 5, figs. 1–4 (androconial scales). Text fig. 3 (holotype ♂). Text fig. 4 (male genitalia). Text fig. 5 (female genitalia).

MATERIAL EXAMINED. Portugal, Azores, Pico : 9 ♂, 3 ♀ in coll. VLCA ; Portugal, Azores, Faial : 10 ♂, 5 ♀ in colls. VLCA, M. Meyer.

DESCRIPTION. Forewing length : see table 1. Male upperside ground-colour dark brown, not significantly darker in material from Faial when compared to specimens from Pico ; forewing dark brown spot in s5 always present and sometimes with a small white pupil in Pico specimens, much more weakly expressed and mostly without white pupil to entirely absent in material from Faial ; spot in s2 usually clearly visible in Pico material, mostly hardly noticeable or absent in Faial material ; basal and discal area only occasionally of a lighter colour than remainder of wing ; sex brand reduced to vestigial, but always at least traces of it ; whitish postdiscal band on underside hindwing clearly visible on upperside. Female forewing upperside basal and discal area lighter, but not distinctly so, than remainder of wing ; markings on upperside forewing more complete than in male, usually somewhat obliterated in Faial specimens. Underside forewing pale to middle ochreous colour, without significant differences between Pico and Faial specimens. No differences in both male and female genitalia between Pico and Faial specimens, no significant differences in androconial scales, which are small (plate 5, see also Oehmig, 1983 : 155, fig. 3).

DISTRIBUTION. Limited to the islands of Pico and Faial.

COMMENTS. The small differences between specimens from both islands, especially in the expression of the spots in s2 and s5 on male upperside forewing, do not justify their subspecific separation (in doing so, one could for instance recognize several subspecies of *H. senthes* on the Aegean islands alone!). On the contrary, they appear much more alike than compared to material from the remaining islands of the central and western groups, that is listed under the next subspecies.

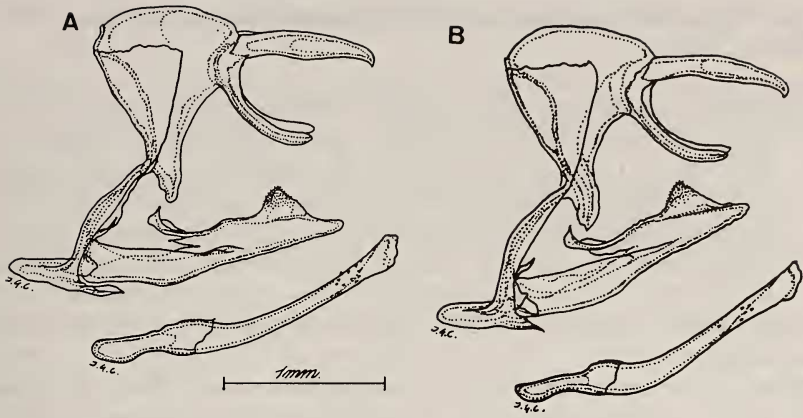


Fig. 4. *Hipparchia (azorina) azorina azorina* (Strecker, 1899) : male genitalia. A. Portugal, Azores, Pico, Chã do Pelado (800 m), 15.VIII.1990, leg. M. Meyer, in coll. VLCA (Prep. JGC no. 2815). B. Portugal, Azores, Faial, Caldeira Cabeço Gordo (900 m), 12.VIII.1990, leg. M. Meyer, in coll. VLCA (Prep. JGC no. 2810).

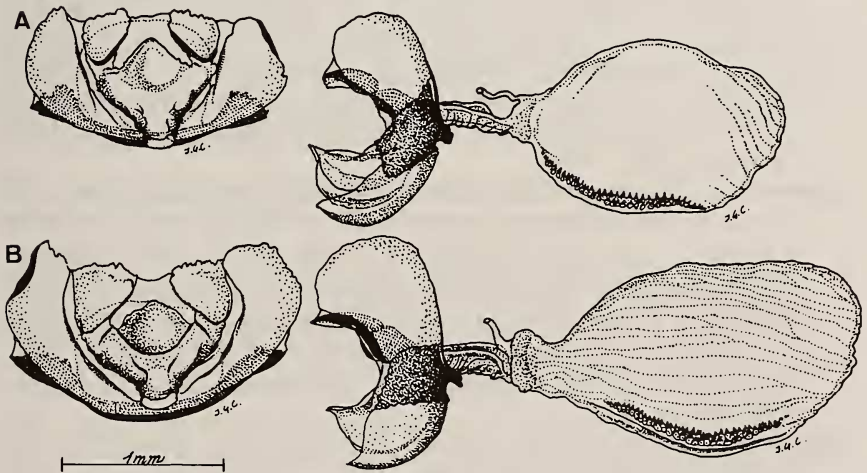


Fig. 5. *Hipparchia (azorina) azorina azorina* (Strecker, 1899) : female genitalia. A. Portugal, Azores, Pico, Chã do Pelado (800 m), 14.VIII.1990, leg. M. Meyer, in coll. VLCA (Prep. JGC no. 2816). B. Portugal, Azores, Faial, Caldeira Cabeço Gordo (900 m), 12.VIII.1990, leg. et coll. M. Meyer (Prep JGC no. 2812).

4.1.2. *Hipparchia (azorina) azorina occidentalis* Bivar de Sousa, 1982, comb. n., stat. n.

“*Hipparchia (Parahipparchia) azorina* (Strecker) ssp. *occidentalis*” Bivar de Sousa, 1982. — *Bolm. Soc. port. Ent.* 7 (Supl. A) : 208–209, 211, figs. 3, 6, 212, figs. 9, 12, 213, figs. 14, 16. Locus typicus : Azores, Flores, “Planalto junto à Caldeira Funda”. Type material : holotype ♂, paratypes 8 ♂, 2 ♀, in coll. Bivar de Sousa, single male paratypes in Museu Bocage (Faculdade de Ciências de Lisboa), Instituto Universitário dos Açores (Laboratório de Ecologia Aplicada), SPEN (Sociedade portuguesa de Entomologia).

“*Hipparchia azorina* (Strecker) ssp. *cenjonatura* n. ssp.” Bivar de Sousa, 1982. — *Bolm. Soc. port. Ent.* 25 : 20. Locus typicus : Azores, São Jorge. — Unavailable name (Article 13(a) of ICZN). Nomen nudum, **syn. n.**

“*Hipparchia azorina jorgense* Oehmig new subspecies” Oehmig, 1983. — *J. Res. Lepidopt.* 20 (3) (1981) : 143–146, Pl. I, figs. a–d, 155, fig. 3, 158, fig. 6.5, 159, fig. 7.4. Locus typicus : Azores, São Jorge. Type material : holotype ♂, paratypes 1 ♂, 8 ♀, in coll. Oehmig. — Junior subjective synonym of *Hipparchia (Parahipparchia) azorina* (Strecker) ssp. *occidentalis* Bivar de Sousa, 1982, **syn. n.**

“*Hipparchia caldeirensis* Oehmig new species” Oehmig, 1983. — *J. Res. Lepidopt.* 20 (3) (1981) : 148–150, Pl. I, figs. o–r, 156, fig. 4.3, 158, fig. 6.1, 159, fig. 7.1. Locus typicus : Azores, Flores, “Caldeira Seca”. Type material : holotype ♂, paratypes 33 ♂, 6 ♀, in coll. Oehmig. — Junior subjective synonym of *Hipparchia (Parahipparchia) azorina* (Strecker) ssp. *occidentalis* Bivar de Sousa, 1982 (Kudrna, 1986 : 186).

“*Hipparchia (Parahipparchia) azorina* (Strecker) ssp. *barbara* Bivar de Sousa n. ssp.” Bivar de Sousa, 1985. — *Bolm. Soc. port. Ent.* 4 (Supl. 1) : 378–379, 381, figs. 1–4, 382, fig. 9. Locus typicus : Azores, Terceira. Type material : holotype ♂, paratypes 13 ♂, 4 ♀, depository not mentioned (presumably at least partly in coll. Bivar de Sousa). — Junior subjective synonym of *Hipparchia (Parahipparchia) azorina* (Strecker) ssp. *occidentalis* Bivar de Sousa, 1982, **syn. n.**

“*Hipparchia (Parahipparchia) azorina* (Strecker) ssp. *minima* Bivar de Sousa n. ssp.” Bivar de Sousa, 1985. — *Bolm. Soc. port. Ent.* 4 (Supl. 1) : 379–380, 381, figs. 5–8, 382, fig. 10. Locus typicus : Azores, Corvo. Type material : holotype ♂, paratypes 9 ♂, 2 ♀, depository not mentioned (presumably at least partly in coll. Bivar de Sousa). — Junior subjective synonym of *Hipparchia (Para-*

hipparchia) *azorina* (Strecker) ssp. *occidentalis* Bivar de Sousa, 1982, **syn. n.**

“[*Hipparchia*] *caldeirensis*” Balletto *et al.*, 1990. — *Atti Convegno Lincei* 85 : 185, 186, 189. — Subsequent misspelling of the name *caldeirensis* Oehmig, 1983.

“*Hipparchia azorina barbarensis*” Tolman & Lewington, 1997. — Collins Field Guide. Butterflies of Britain and Europe : 195, 311. — Subsequent misspelling of the name *barbara* Bivar de Sousa, 1985.

ILLUSTRATIONS. Plate 3, figs. 3 & 6–12. Plate 6, figs. 1–4 (androconial scales). Text figs. 6–7 (male genitalia). Text figs. 8–9 (female genitalia). MATERIAL EXAMINED. Portugal, Azores, Flores : 6 ♂, 3 ♀ in coll. VLCA ; Portugal, Azores, São Jorge : 4 ♂, 2 ♀ in colls. VLCA, M. Meyer ; Portugal, Azores, Terceira : 8 ♂, 4 ♀ in coll. VLCA.

DESCRIPTION. Forewing length : see table 1. Upperside forewing dark brown spot in s5 always, in s2 usually present ; basal and discal area in both sexes markedly lighter than remainder of wing, much more so than in nominotypical *azorina*, sex brand entirely absent, in material from São Jorge sometimes traces of it ; postdiscal band underside hindwing white, sharply contrasting and hence even more apparent on upperside than in nominotypical *azorina*. Both male and female genitalia not significantly different from nominotypical *azorina*. Androconial scales unknown in material from Flores, but detected in specimens from Corvo, São Jorge and Terceira ; individually (and perhaps to some extent geographically) variable, though not significantly different from nominotypical *azorina* from Pico and Faial (plate 6, see also figs. in Oehmig, 1983 and Bivar de Sousa, 1985b).

DISTRIBUTION. Known from the islands of Flores and Corvo (western group) and from São Jorge and Terceira (central group).

COMMENTS. Material from these islands shows some similarities in external features that may indicate a common origin, as opposed to nominotypical *azorina* (alternatively, these may have been acquired independently as a result of comparable environmental pressures). Such a treatment is certainly more informative than the naming of each and every island population and it may be testable in the future (e. g. with the aid of molecular techniques). Characters purported to differentiate the taxa *jorgense*, *barbara* and *minima* are part of the range of variation of *occidentalis*. Oehmig (1983) noted some differences in the number of micropyles and ribs in the eggs of “*H. caldeirensis*” and “*H. azorina ohshimai*” (and *H. miguelensis*), largely basing his

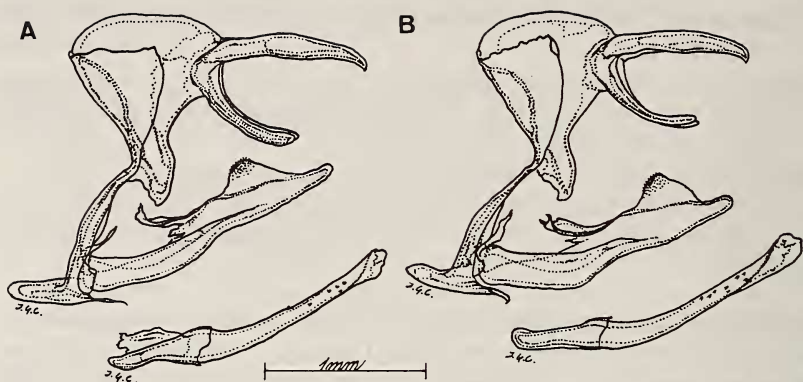


Fig. 6. *Hipparchia (azorina) azorina occidentalis* Bivar de Sousa, 1982 : male genitalia. A. Portugal, Azores, Flores, Caldeira Comprida (580 m), 8.VIII.1990, leg. M. Meyer, in coll. VLCA (Prep. JGC no. 2797). B. Portugal, Azores, Terceira, Serra de Santa Barbara (1000 m), 19.VIII.1990, leg. M. Meyer, in coll. VLCA (Prep. JGC no. 2801).

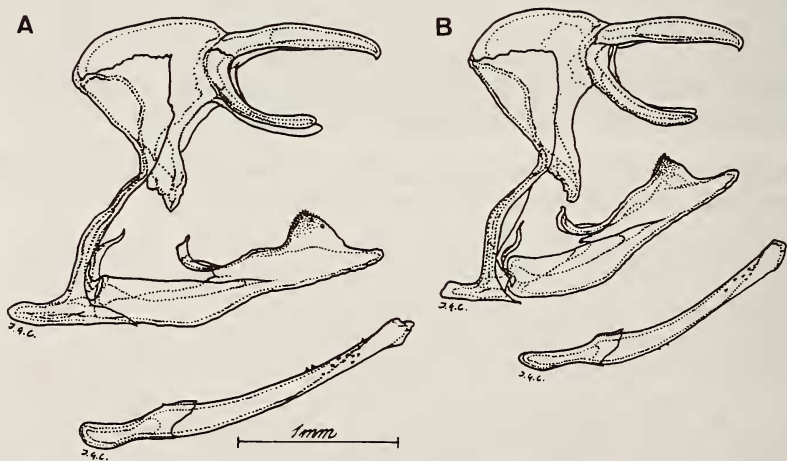


Fig. 7. *Hipparchia (azorina) azorina occidentalis* Bivar de Sousa, 1982 : male genitalia. A. Portugal, Azores, São Jorge, Serra do Topo, Pedra Vermelha (800 m), 17.VII.1990, leg. M. Meyer, in coll. VLCA (Prep. JGC no. 2805 ; specimen illustrated on plate 3, fig. 8). B. same data as A (Prep. JGC no. 2806).

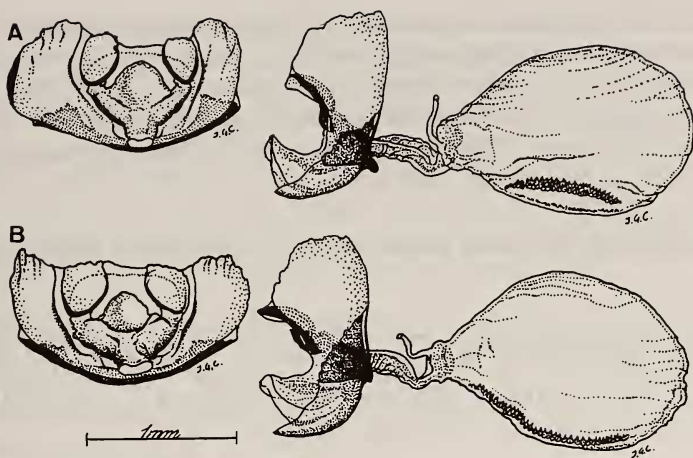


Fig. 8. *Hipparchia (azorina) azorina occidentalis* Bivar de Sousa, 1982 : female genitalia. A. Portugal, Azores, Flores, Caldeira Comprida (580 m), 8.VIII.1990, leg. M. Meyer, in coll. VLCA (Prep. JGC no. 2799 ; specimen illustrated on plate 3, fig. 10). B. same data as A (Prep. JGC no. 2800 ; specimen illustrated on plate 3, fig. 6).

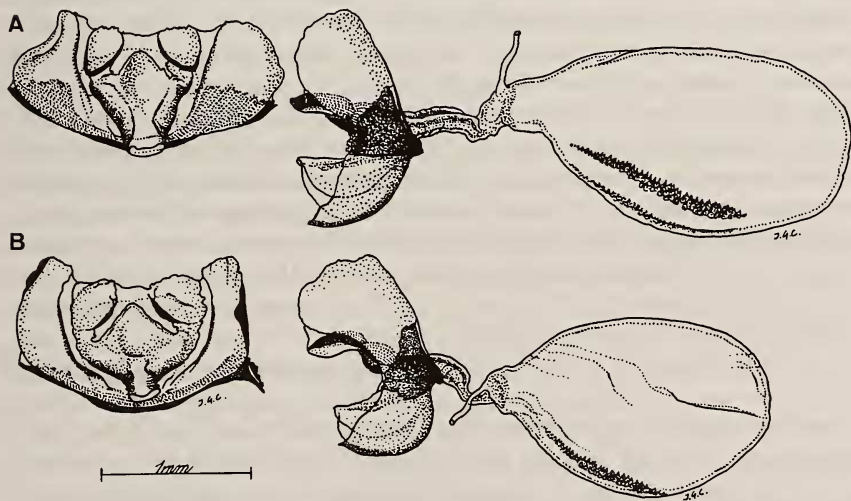


Fig. 9. *Hipparchia (azorina) azorina occidentalis* Bivar de Sousa, 1982 : female genitalia. A. Portugal, Azores, São Jorge, Serra do Topo, Pedra Vermelha (800 m), 17.VIII.1990, leg. et coll. M. Meyer (Prep. JGC no. 2809). B. Portugal, Azores, Terceira, Serra de Santa Barbara (1000 m), 18.VIII.1990, leg. M. Meyer, in coll. VLCA (Prep. JGC no. 2803 ; specimen illustrated on plate 3, fig. 12).

argument for the specific separation of these taxa on such data. These, however, can vary substantially within a single species, e. g. in *H. semele*, but also in other *Hipparchia* species and in the Satyrini in general (Wagener, 1983 ; García-Barros & Martín, 1991, 1995 ; Thomson, 1992 ; Jutzeler, Grillo & de Bros, 1995 ; Jutzeler, Pitzalis & de Bros, 1995 ; Jutzeler *et al.*, 1997).

4.2. *Hipparchia (azorina) miguelsensis* (Le Cerf, 1935) comb. n., stat. n.

“*Satyrus azorinus* Strecker, ssp. *miguelsensis*, nova” Le Cerf, 1935. — *Bull. Soc. ent. Fr.* 40 : 207–208, Pl. V, figs. 1–5. Locus typicus : Azores, São Miguel. Type material : syntypes 3 ♂, 1 ♀, in Muséum National d’Histoire Naturelle, Paris.

ILLUSTRATIONS. Plate 3, figs. 13–15. Plate 7, figs. 1–4 (androconial scales). Text fig. 10 (male genitalia). Text fig. 11 (female genitalia).

MATERIAL EXAMINED. Portugal, Azores, São Miguel : 21 ♂, 7 ♀ in colls. VLCA, H. Henderickx.

DESCRIPTION. Forewing length : see table 1 ; both sexes larger than *H. (azorina) azorina*. Wings more elongated than in *H. (azorina) azorina*, forewing usually with pointed apex and convex outer margin, unlike any other taxon treated in the present study. Male upperside ground-colour dark brown, of a warmer tinge than in *H. (azorina) azorina* ; basal and discal area of forewing as dark as rest of wing, dark brown spots in s2 and s5 always visible, often encircled by a diffuse orange-ochreous patch that is usually quite reduced, but sometimes more extended and in a few cases well-expressed, occasionally an additional spot in s3, also encircled by an orange-ochreous patch ; sex brand vestigial but always present in s2, (nearly) touching median vein of cell, sometimes additional traces in s1b ; hindwing dark spot in s2 always present, often encircled by an orange-ochreous patch, additional small orange-ochreous patches in s3–s5 variously expressed, from entirely absent to well marked ; one specimen has an additional dark spot in s3. Female similar to male but markings usually more complete, creamy yellow, with distinctly lighter basal and discal area. Underside forewing in both sexes usually more vividly ochreous than in *H. (azorina) azorina*. Underside hindwing discal line bending much more gently distally in s4–s5 than in *H. (azorina) azorina*, evenly rounded (sometimes pointed in female), whitish postdiscal band much narrower than in *H. (azorina) azorina* (and hence less conspicuous on upperside hindwing). Male genitalia larger than in *H. (azorina)*

azorina, uncus > tegumen (1.1×), valve and especially gnathos longer than in most *H. (azorina) azorina*, dorsal spines on aedeagus usually better developed and extending more basad than in *H. (azorina) azorina*. Female genitalia sterigma with mid-dorsal process narrower at base, more elongated and pointed distally, unlike *H. (azorina) azorina* except for one female from Pico (Prep. No. 2547), corpus bursae larger and signum longer than in *H. (azorina) azorina*. Androconial scales more elongated than in *H. (azorina) azorina* (plate 7, see also Bivar de Sousa, 1982a, 1985b ; Oehmig, 1983).

DISTRIBUTION. Restricted to the island of São Miguel (eastern island group). Old records of "*Satyrus Janira*" from Santa Maria (Morelet, 1860 ; Drouët, 1861 ; Godman, 1870) could refer to *miguelensis*, but recent explorations (Bivar de Sousa, 1985b ; Meyer, 1991) failed to confirm its presence on the latter island.

BIONOMICS. In natural grasslands with *Festuca jubata*, the larval host-plant (according to Fuchs, 1993, *F. petraea*), from 600 m to 1100 m (for further details see Oehmig, 1983 and Fuchs, 1993). Univoltine : adults from June (Le Cerf, 1935 ; Oehmig, 1983) to September (Oehmig, 1983 ; Vieira & Silva, 1994). Early stages : described in detail by Oehmig (1983).

COMMENTS. It was Oehmig (1983) who first raised this taxon to species rank. In this he was followed by all subsequent authors except Bivar de Sousa (1985b), who still considered it to be a subspecies of *azorina*. *H. (azorina) miguelensis* differs significantly from all populations from the central and western Azores in wing shape, markings, male and female genitalia and androconial scales, suggesting a substantial degree of genetic differentiation, while closely related to *H. (azorina) azorina* phylogenetically and biologically (same larval host-plant) at the same time. For this reason we consider the superspecies concept sensu Mayr (1963), with two component species as recognized here, to apply convincingly to the present case.

5. The *Hipparchia aristaeus* group

DESCRIPTION. The four recognized taxa composing this group are quite distinct in wing markings. *H. maderensis*, *H. algerica* and *H. aristaeus* have quite similar genitalia, while those of *H. senthes* are distinct. A full description will be presented under each nominal taxon.

DISTRIBUTION. Madeira (*H. maderensis*) ; Morocco, Algeria, Tunisia (*H. algerica*) ; Corsica, Sardinia, Elba, Giglio, Capraia (*H. aristaeus*) ; Sicily, S. Italy, Albania, Former Yugoslav Republic of Macedonia,

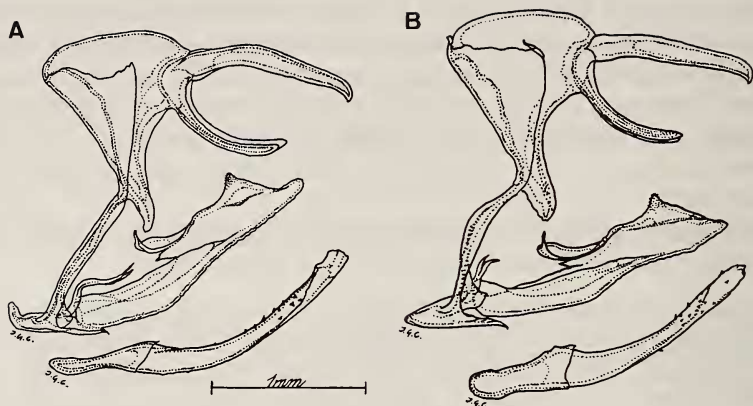


Fig. 10. *Hipparchia (azorina) miguelensis* (Le Cerf, 1935) : male genitalia.
 A. Portugal, Azores, São Miguel, Serra de Agua de Pau (900 m), 22.VII.1994, leg. H. Henderickx, in coll. VLCA (Prep. JGC no. 2545 ; specimen illustrated on plate 3, fig. 13). B. Portugal, Azores, São Miguel, Serra de Agua de Pau (900 m), 24.VII.1994, leg. H. Henderickx, in coll. VLCA (Prep. JGC no. 2818).

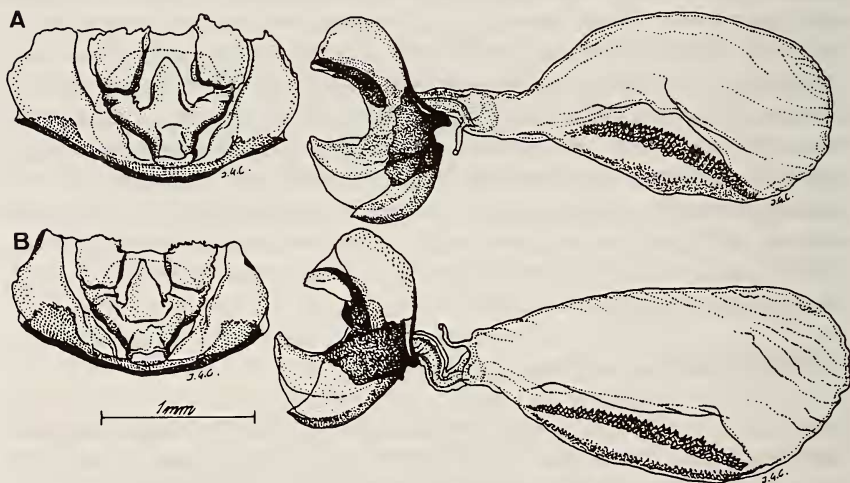


Fig. 11. *Hipparchia (azorina) miguelensis* (Le Cerf, 1935) : female genitalia.
 A. Portugal, Azores, São Miguel, Serra de Agua de Pau (900 m), 22.VII.1994, leg. H. Henderickx, in coll. VLCA (Prep. JGC no. 2821). B. Portugal, Azores, São Miguel, Serra de Agua de Pau (900 m), 24.VII.1994, leg. H. Henderickx, in coll. VLCA (Prep. JGC no. 2822 ; specimen illustrated on plate 3, fig. 15).

S. Bulgaria, Greece including the Aegean islands, western half of Turkey (*H. senthes*).

COMMENTS. Since de Lattin (1949), the taxa of this group have been considered by most authors to form an entity on their own (de Lattin treated *H. maderensis* as a species distinct from the remaining "races" of *H. aristaeus*), either as full (morpho-)species (Kudrna, 1984, 1986, 1996; Taymans, 1989; Balletto *et al.*, 1990; Cesaroni *et al.*, 1994; Balletto, 1995) or as subspecies (Verity, 1953a, 1953b (using the term "eserge" [exerge], under *Hipparchia semele*); Higgins & Riley, 1970, 1984; Higgins, 1975; Kudrna, 1977; Higgins & Hargreaves, 1983; Coutsis, 1984; Hesselbarth, van Oorschot & Wagener, 1995; De Prins & Iversen, 1996; the latter authors erroneously treat *H. sbordonii* as a subspecies of *H. aristaeus* though it clearly belongs to the *H. semele* group, cf. Kudrna, 1984; Balletto *et al.*, 1990; Cesaroni *et al.*, 1994). Balletto *et al.* (1990) carried out a cladistic analysis of the subgenus *Parahipparchia*: in the resulting cladogram, the *H. aristaeus* group comes out as a monophyletic unit. According to that study, the original set of 27 multistate characters includes two characters purported to define this group, viz. the "sclerotized ductus bursae" and the "small sterigma" (although, in both cases, "*H. ballettoi*" is excluded); one other character ("[length of] uncus = [length of] tegumen") is shared with *miguelensis* and one more ("mid-dorsal process intermediate") is shared with *azorina*, *occidentalis* and *miguelensis*. Our own analysis does not support the usefulness of any of these characters as a possible synapomorphy (see below, section 7). Cesaroni *et al.* (1994) studied the evolutionary relationships among 17 Mediterranean populations belonging to eight *Parahipparchia* taxa (they synonymized a ninth and obtained congruent relationships among taxa from allozymes and male genital morphometrics: three taxa of the *aristaeus* group (*aristaeus*, *algerica* and "*ballettoi*") clustered together in both analyses. As we have been unable to find any convincing synapomorphy supporting the monophyly of the *aristaeus* group, it is very well possible that it is paraphyletic, either with or without the inclusion of superspecies *H. azorina*. We feel therefore compelled to treat it as such without conclusive support for its monophyly, albeit in doing so we follow common practice, that is based on overall similarity in structural characters and strict allopatry of the individual taxa. Evidence based on morphology, allozymes and ecology supports their status as full species (Cesaroni *et al.*, 1994; this study).

5.1. *Hipparchia maderensis* (Baker, 1891)

- “*Satyrus semele v. maderensis*” Baker, 1891. — *Trans. ent. Soc. Lond.* 1891 : 202, 221, Plate XII, fig. 2, 2a. Locus typicus : Madeira. Type material : lectotype ♂, paralectotypes 11 ♂, 2 ♀, in British Museum (Natural History), London [now The Natural History Museum, London]; design. Kudrna (1977 : 106).
- “*Satyrus semele maderensis*” Cockerell, 1923. — *Entomologist* 56 : 246. Subsequent misspelling of the name *maderensis* Baker, 1891.
- “*Hipparchia (Parahipparchia) mederensis*” Balletto *et al.*, 1990. — *Atti Convegno Linnei* 85 : 173. — Subsequent misspelling of the name *maderensis* Baker, 1891.
- “*Hipparchia (Parahipparchia) madeirensis*” Balletto *et al.*, 1990. — *Atti Convegno Linnei* 85 : 186. — Subsequent misspelling of the name *maderensis* Baker, 1891.

ILLUSTRATIONS. Plate 4, figs. 1–2. Plate 8, figs. 1–4 (androconial scales). Text fig. 12 (male genitalia). Text fig. 13 (female genitalia).

MATERIAL EXAMINED. Portugal, Madeira : 168 ♂, 96 ♀ in colls. VLCA, ZMA.

DESCRIPTION. Forewing length : see table 1 ; both sexes larger than superspecies *H. azorina*, but slightly smaller than *H. algerica* and *H. aristaeus*, except females of last taxon from Corsica (but there $n = 14!$). Male upperside ground-colour dark brown, wing markings on upperside forewing much reduced to completely absent, except for the omnipresent blackish brown spots in s2 and s5, the latter one sometimes with a white pupil, but usually at least some traces of the orange-ochreous markings, though less so than in the better marked specimens of *H. (azorina) miguelensis* ; sex brand well developed, covering much of the cell except its base, and the basal part of s5 down to s1b, even invading s1a ; hindwing dark spot in s2 always present, usually with white pupil and usually encircled by an orange-ochreous patch, additional small orange-ochreous patches in s3–s5 usually vestigial but present, rarely better marked, but even more rarely entirely absent. Female similar to male but markings more complete, creamy yellow to orange-ochreous, basal and discal area upperside forewing not significantly lighter ; orange-ochreous patches on upperside hindwing rarely forming a complete row, often absent in s3–s4. Underside forewing in both sexes more vividly ochreous than in *H. (azorina) azorina* and most *H. (azorina) miguelensis*, basal-discal area corresponding to area of sex brand of upperside more orange in males, in the females also darker ochreous than postdiscal area, sharply bordered

distally by blackish brown discal line. Underside hindwing discal line gently bending distally in s4–s5, evenly rounded to pointed in male, usually more pointed in female; whitish postdiscal band well expressed, often invaded by greyish mottling, especially in the females. Male genitalia invariably larger than in superspecies *H. azorina*, both overall and in size of the individual parts; uncus > tegumen (1.1); valve with prominent, pointed dorsal process; aedeagus more curved than in superspecies *H. azorina*; without any spines. Female genitalia overall size of sterigma approximately as large to slightly larger than in superspecies *H. azorina*, but dorsal lamella always larger; mid-dorsal process either narrow or wide at base, but always short; ductus bursae and cervix bursae as a rule more heavily sclerotized than in superspecies *H. azorina*; corpus bursae much larger than in superspecies *H. azorina* and slightly larger than in *H. algerica* and *H. aristaeus* (except for 1 ♀ from Corsica), signum very long, much more than in superspecies *H. azorina* and slightly longer than in *H. algerica*. Androconial scales not significantly different from *H. (azorina) azorina*, shorter than in *H. (azorina) miguelensis* (plate 8).

DISTRIBUTION. Restricted to the island of Madeira (Portugal).

BIONOMICS. Most commonly associated with areas of light (conifer) woodland with extensive grass and herb layers which also contain both bare earth and abundant nectar sources (especially *Origanum* and *Rubus* species), generally at mid-altitudes, between 800 and 1200 m, particularly in the south and southwestern parts of the island (Smith & Shreeve, 1990). Oehmig (1977) records the species from *Airopsis* meadows from 1400 m up to the highest summits, but sometimes lower, sitting on the trunks of pine trees in the forest zone, while Swash & Askew (1982) mention similar habitats with *Erica arborea* L. and bracken. One of us (AO) observed the butterfly in the field between 20.VII and 1.VIII.1993. It was particularly common near Poiso (1300–1350 m) and also relatively frequent at Eira do Serrado (1000–1500 m) and in the Pico do Areeiro-Pico Ruivo area (1750–1800 m). Adults were taking nectar on flowers of *Rubus* and *Origanum*, at Eira do Serrado on blossoms of the imported *Castanea sativa* Mill., a behaviour also reported by Meyer (1993). Males were often perching, mostly on rocks. Females occurred in the same habitats as the males, though generally larger aggregations were encountered in more bushy and grassy spots, while the males tended to congregate on more open, bare locations. A few specimens were recorded at lower altitudes (600–700 m) at Curral das Freiras. Larval host-plants: unknown. Smith & Shreeve (1990) observed egg-laying at Poiso: eggs

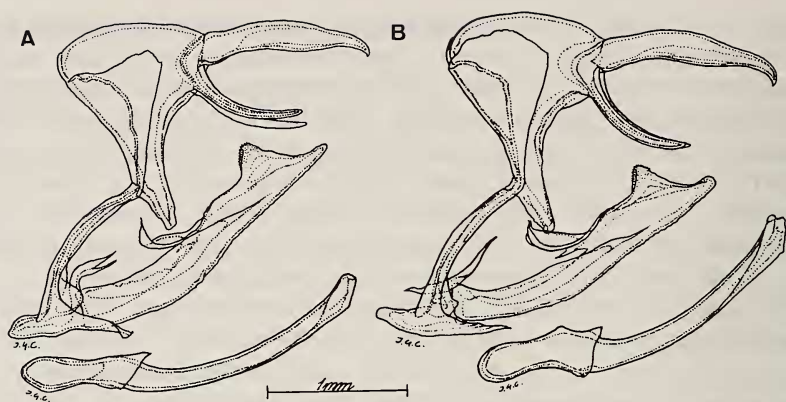


Fig. 12. *Hipparchia maderensis* (Baker, 1891) : male genitalia.

A. Portugal, Madeira, 2 km SW. Poiso (1350 m), 25.VII.1993, leg. A. Olivier, in coll. VLCA (Prep. JGC no. 2533). B. same data as A (Prep. JGC no. 2536).

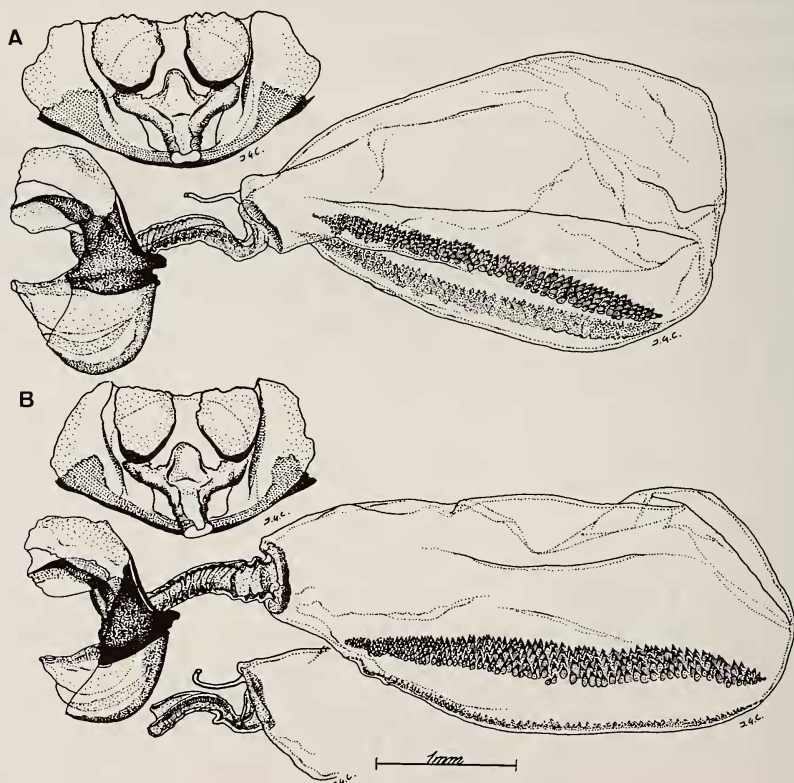


Fig. 13. *Hipparchia maderensis* (Baker, 1891) : female genitalia.

A. Portugal, Madeira, 2 km SW. Poiso (1350 m), 21.VII.1993, leg. A. Olivier, in coll. VLCA (Prep. JGC no. 2540). B. same data as A (Prep. JGC no. 2541).

were placed low (< 10 mm) on green shoots of a *Holcus* grass species, dry stems, and exposed roots of an *Agrostis* species. Oehmig (1977) records the grass species *Aira praecox*, *Aira caryophyllea* and *Agrostis castellana* as likely host-plants. For further details about the habitat etc. see Walker (1931), Rebel (1939b), Martin (1941), Kudrna (1977), Oehmig (1977), Swash & Askew (1982), Higgins & Riley (1984), Bivar de Sousa (1986), Meyer (1993) and, especially, Smith & Shreeve (1990). Univoltine : adults usually flying from mid-July (Rebel, 1939b) to late September (Kudrna, 1977 ; Smith & Shreeve, 1990), but there are reports from mid-June onwards (Martin, 1941 ; Kudrna, 1977 ; Swash & Askew, 1982) as well. Early stages : no published description, though Hesselbarth, van Oorschot & Wagener (1995 : 900) mention "einer von HESSELBARTH (unveröff.) durchgeführten Zucht von *maderensis*" without details and Aussem (1980) presents limited data on the mandibles of larvae of *H. maderensis*.

COMMENTS. Felder (1862) first reported this taxon from Madeira as "*Satyrus Semele* Lin.", followed by Lang (1884), and Baker (1891) described it as "*Satyrus semele* v. *maderensis*" (in modern terms as a subspecies of *Hipparchia semele*), a treatment that was adopted by all subsequent early authors (Tutt, 1896 ; Staudinger & Rebel, 1901 ; Kirby, 1903 ; Seitz, 1908 ; Stauder, 1915–1916 ; Rebel, 1917, 1939b, 1940a, 1940b ; Cockerell, 1923 ; Verity, 1923–1924 ; Walker, 1931 ; Gaede, 1931 and Martin, 1941). It was de Lattin (1949) who established distinct species status for it and who emphasized its closer affinity to *H. aristaeus* rather than to *H. semele*. In this he was followed by de Lesse (1951, 1952), Varin (1960), Kostrowicki (1969), Kudrna (1975, 1984, 1986, 1996), Taymans (1989), Balletto *et al.* (1990), D'Abrera (1992), Meyer (1993), Balletto (1995), Jutzeler *et al.* (1997) and Dennis (1997), though fairly recently Manley & Allcard (1970) and Fonteneau (1971) continued to consider it as a subspecies of *H. semele*. Leestmans (1968) and Higgins & Riley (1970, 1984) downgraded *maderensis* to a subspecies of *H. aristaeus* and since then most authors have treated it as such (or as a subspecies of *H. algerica*, i. e. Zangheri, 1975 ; Higgins, 1975 ; Kudrna, 1977 ; Oehmig, 1977 ; Heath, 1981 ; Swash & Askew, 1982 ; Higgins & Hargreaves, 1983 ; Coutsis, 1984 ; Lace & Jones, 1984 ; Bivar de Sousa, 1986 ; Karsholt, 1988 ; Smith & Shreeve, 1990 ; Fernández-Rubio, 1991 ; Owen & Smith, 1994 ; Hesselbarth, van Oorschot & Wagener, 1995 ; Tolman & Lewington, 1997). Finally, Bernardi (1961 ; and Leestmans, 1975 after him) listed *maderensis* as belonging to a superspecies *H. aristaeus* (vide supra, Section 4, opening part for critical discussion). The genitalia of *H. maderensis* are obviously quite similar to those of *algerica* and *aristaeus*, though

Plate 1. *Hipparchia senthes* (Fruhstorfer, 1908) : type specimens of various nominal taxa.

1. *Satyrus semele blachieri* Fruhstorfer, 1908. Lectotype ♀. “*semele blachieri* Fruhst.” [handwritten]/“Ch. Blachier” [printed]/“Sicile” [handwritten]/“Type” [printed]/“LECTO-TYPE” [printed]/“*Satyrus semele blachieri* Fruhstorfer, 1908. LECTOTYPE design. Kudrna (1977 : 109) ; illustr. Olivier & Coutsis (1997 : Plate 1, fig. 1)” [red label, printed], in Muséum d’Histoire Naturelle, Genève.

2. *Satyrus semele blachieri* Fruhstorfer, 1908. Paralectotype ♀. “Coll. Blachier” [printed]/“Sicile” [printed]/“PARA-LECTO-TYPE” [printed]/“*Satyrus semele blachieri* Fruhstorfer, 1908. PARALECTOTYPE design. Kudrna (1977 : 109) ; illustr. Olivier & Coutsis (1997 : Plate 1, fig. 2)” [red label, printed], in Muséum d’Histoire Naturelle, Genève.

3. *Satyrus Semele*, Linné, race *Siciliana* Oberthür, 1914. Lectotype ♀. “*Semele-Siciliana* Obthr. ♀” [handwritten]/uncoloured figure of the specimen with number “2315” [printed, proof copperplate of Oberthür, 1914 : Plate CCLXXXIV, fig. 2315]/“Ex. Coll. Bellier” [printed]/“Ex Oberthür Coll. Brit. Mus. 1927-3.” [printed]/“Sicile” [handwritten]/“Specimen” [printed] “A” [handwritten]/“TC1” [printed] “77” [handwritten]/“13/11-12” [handwritten]/“SYNTYPE *Satyrus semele siciliana* Oberthür” [handwritten] det. P.R. Ackery 197” [printed] “7” [handwritten]/“SYN-TYPE” [printed] “*Satyrus Semele-Siciliana* Oberthür, 1914. LECTOTYPE design. Olivier & Coutsis (1997) ; illustr. Olivier & Coutsis (1997 : Plate 1, fig. 3)” [red label, printed], in The Natural History Museum, London.

4. *Satyrus Semele*, Linné, race *Siciliana* Oberthür, 1914. Paralectotype ♀. “*Semele-Siciliana* Obthr. ♀” [handwritten]/uncoloured figure of the specimen with number “2316” [printed, proof copperplate of Oberthür, 1914 : Plate CCLXXXIV, fig. 2316]/“Ex Coll. Bellier” [printed]/“Ex Oberthür Coll. Brit. Mus. 1927-3.” [printed]/“Sicile” [handwritten]/“Specimen” [printed] “B” [handwritten]/“TC1” [printed] “77” [handwritten]/“SYNTYPE *Satyrus semele siciliana* Oberthür” [handwritten] det. P.R. Ackery 197” [printed] “7” [handwritten]/“SYN-TYPE” [printed] “SYN-TYPE” [printed] “*Satyrus Semele-Siciliana* Oberthür, 1914. PARALECTOTYPE design. Olivier & Coutsis (1997) ; illustr. Olivier & Coutsis (1997 : Plate 1, fig. 4)” [red label, printed], in The Natural History Museum, London.

5. *Satyrus semele* L. f. *neapolitana* Stauder, 1921. Lectotype ♂. “*neapolitana* Str.” [handwritten]/“Ital. mer.” [printed] “300” [handwritten] “m. penins. Surrentina M. Faito” [printed] “14.6” [handwritten] “192” [printed] “0” [handwritten] “H. Stauder legit.” [printed + vertically handwritten illegible citation]/“C/Roths 10/11” [printed]/“*Satyrus semele* L. f. *neapolitana* Stauder, 1921. LECTOTYPE design. Olivier & Coutsis (1997) ; illustr. Olivier & Coutsis (1997 : Plate 1, fig. 5)” [red label, printed], in The Natural History Museum, London (genitalia illustrated on text fig. 30).

6. *Satyrus semele* L. f. *neapolitana* Stauder, 1921. Paralectotype ♂. “Ital. mer.” [printed] “400” [handwritten] “m. penins. Surrentina M. Faito 192” [printed] “0” [handwritten] “H. Stauder legit.” [printed + handwritten “10/6” to the left of main text]/“B/Roths 10/11” [printed]/“*Satyrus semele* L. f. *neapolitana* Stauder, 1921. PARALECTOTYPE design. Olivier & Coutsis (1997) ; illustr. Olivier & Coutsis (1997 : Plate 1, fig. 6)” [red label, printed], in The Natural History Museum, London.

7. *Satyrus semele* L. f. *neapolitana* Stauder, 1921. Paralectotype ♀. “Ital. mer.” [printed] “800” [handwritten] “m. penins. Surrentina M. Faito” [printed] “1.7” [handwritten] “192” [printed] “0” [handwritten] “H. Stauder legit.” [printed] “K/Roths 10/11” [printed] “*Satyrus semele* L. f. *neapolitana* Stauder, 1921. PARALECTOTYPE design. Olivier & Coutsis (1997) ; illustr. Olivier & Coutsis (1997 : Plate 1, fig. 7)” [red label, printed], in The Natural History Museum, London.

8. *Satyrus semele* L. f. *neapolitana* Stauder, 1921. Paralectotype ♀. “Ital. mer.” [printed] “800” [handwritten] “m. penins. Surrentina M. Faito” [printed] “1.7” [handwritten] “192” [printed] “0” [handwritten] “H. Stauder legit.” [printed] “G/Roths 10/11” [printed] “*Satyrus semele* L. f. *neapolitana* Stauder, 1921. PARALECTOTYPE design. Olivier & Coutsis (1997) ; illustr. Olivier & Coutsis (1997 : Plate 1, fig. 8)” [red label, printed], in The Natural History Museum, London.





- Plate 2. *Hipparchia senthes* (Fruhstorfer, 1908) (figs. 1–5 & 7–8, including type specimens of various nominal taxa) and *Hipparchia semele* (Linnaeus, 1758) (fig. 6).
1. *Hipparchia ballettoi* Kudrna, 1984. Holotype ♂. “M. FAITO (NA) 29.VII.80” [handwritten]/“Holo-type” [printed]/“*Hipparchia ballettoi* Kudrna, 1984. HOLO-TYPE ; illustr. Kudrna (1984 : 230, fig. 1) et Olivier & Coutsis (1997, Plate 2, fig. 1)” [red label, printed], in coll. E. Balletto.
 2. *Hipparchia ballettoi* Kudrna, 1984. Paratype ♀. “M.te Faito (SA) 21-VII” [handwritten]/“*Hipparchia ballettoi* Kudrna, 1984. PARATYPE ; illustr. Kudrna (1984 : 230, fig. 2) et Olivier & Coutsis (1997, Plate 2, fig. 2)” [red label, printed], in coll. E. Balletto.
 3. *Hipparchia senthes* (Fruhstorfer, 1908) ♂. Italy, Calabria, Prov. Cosenza, La Sila, Cerenzia (600–650 m), 27.VII.1995, leg. A. Olivier, in coll. VLCA (genitalia illustrated on text fig. 22).
 4. *Hipparchia senthes* (Fruhstorfer, 1908) ♂. Italy, Calabria, Prov. Cosenza, La Sila, Cerenzia (600–650 m), 27.VII.1995, leg. A. Olivier, in coll. VLCA.
 5. *Hipparchia senthes* (Fruhstorfer, 1908) ♂. Italy, Sicily, Prov. Palermo, Monti Le Madonie, Cozzo Pomieri, 7 km NW. Petralia Sottana (1150–1300 m), 17.VII.1991, leg. A. Olivier, in coll. VLCA (genitalia illustrated on text fig. 21).
 6. *Satyrus semele* L. f. *blachierioides* Stauder, 1921. Lectotype ♂. “Calabria mer. Aspromonte” [printed] “900” [handwritten] “m.” [printed] “3.VII” [handwritten] “192” [printed] “0” [handwritten] “H. Stauder legit.” [printed + handwritten vertically “Polsi”]/“D/Roths 10/11” [printed]/“*Satyrus semele* L. f. *blachierioides* Stauder, 1921. LECTOTYPE design. Olivier & Coutsis (1997) ; illustr. Olivier & Coutsis (1997 : Plate 2, fig. 6)” [red label, printed], in The Natural History Museum, London (genitalia illustrated on text fig. 31).
 7. *Eumenis (Satyrus) semele senthes* Fruhstorfer, 1908. Lectotype K. “*semele senthes* Fruhst.” [handwritten]/“*Eumenis semele senthes* Fruhstorfer 1908 O Kudrna dd.” [handwritten]/“Griechenland Fruhstorfer” [printed]/“Fruhstorfer Coll. B.M. 1937–285” [printed]/“Taygetos” [handwritten]/“Specimen” [printed] “C” [handwritten] “TC1” [printed] “76” [handwritten]/“Type” [printed]/ “LECTOTYPE *Eumenis semele senthes* Fruhstorfer” [handwritten] det. P.R. Ackery 197” [printed] “7” [handwritten]/ “LECTOTYPE” [printed]/“LECTO-TYPE” [printed]/“2639” [handwritten]/“Androconia” [printed] “061” [handwritten]/“*Eumenis (Satyrus) semele senthes* Fruhstorfer, 1908. LECTOTYPE design. Kudrna (1977 : 116) ; illustr. Olivier & Coutsis (1997 : Plate 2, fig. 7)” [red label, printed], in The Natural History Museum, London (genitalia illustrated on text fig. 29).
 8. *Eumenis (Satyrus) semele senthes* Fruhstorfer, 1908. Paralectotype ♀. “Griechenland” [handwritten] “Fruhstorfer” [printed] [on the other side handwritten “Krüper”]/“Fruhstorfer Coll. B.M. 1937–285.” [printed]/“Specimen” [printed] “D” [handwritten] “TC1” [printed] “76” [handwritten]/“Type” [printed]/“PARALECTOTYPE *Eumenis semele senthes* Fruhstorfer” [handwritten] det. P.R. Ackery 197” [printed]/ “7” [handwritten]/“PARA-LECTO-TYPE” [printed]/“*Eumenis (Satyrus) semele senthes* Fruhstorfer, 1908. PARALECTOTYPE design. Kudrna (1977 : 116) ; illustr. Olivier & Coutsis (1997 : Plate 2, fig. 8)” [red label, printed], in The Natural History Museum, London.

this similarity may be symplesiomorphic (see Section 5, opening part : Comments). What is clear beyond any doubt is that it certainly is not conspecific with *H. semele*. We treat it as a full species on circumstantial but compelling evidence, viz. mainly total (and presumably long-lasting) geographical isolation, distinct habitat specialization and strongly differentiated external phenotype, in absence of corroborative evidence from allozymes (unlike with the three following species). An analysis of *H. maderensis* in this respect is highly desirable, but we confidently predict that it will add further support to its full species status.

5.2. *Hipparchia algirica* (Oberthür, 1876)

“*Satyrus Semele*, L., var., *Algirica*, OBR.” Oberthür, 1876. — *Études d'Entomologie* 1 : 27. Locus typicus : [Algeria] Daya, Lambèze [Lambessa], Collo. Type material : lectotype ♂, Algérie : Lambessa, in British Museum (Natural History), London [now The Natural History Museum, London] ; design. Kudrna (1977 : 103).

“*Satyrus semele algirica*” Fruhstorfer, 1908. — *Ent. Z., Frankf. a. M.* 22 : 93. — Subsequent misspelling of the name *Algirica* Oberthür, 1876 (see also Chnéour, 1947–1948 [1947] : 22 ; Valletta, 1972 : 38 ; Coene, 1976 : 174 ; Brown, 1977 : 155 ; Devarenne, 1981 : 174 (the latter as “*algericus*”) and Leigheb, 1988 : 122).

“*Hipparchia semele*, L. race *pallidalgirica*, mihi” Verity, 1923. — *Entomologist's Rec. J. Var.* 35 : 155. Locus typicus : Algeria, Lambèze [Lambessa] and Blida. Type material : syntypes 3 ♂ Algeria, Lambese [Lambessa], in Museo Zoologica ‘La Specola’, Firenze. — Junior subjective synonym of *Satyrus Semele*, L., var., *Algirica* Oberthür, 1876 (Kudrna, 1977 : 101).

“*Satyrus semele pallidalgerica*” Gaede, 1930. — Satyridae [part.]. In : Seitz, A. (Ed.) : *Die Gross-Schmetterlinge der Erde. Eine systematische Bearbeitung der bis jetzt bekannten Gross-Schmetterlinge* I. Supplement 1 : 163. — Subsequent misspelling of the name *pallidalgirica* Verity, 1923 (see also Chnéour, 1942 : 54).

“*Hipparchia algyrica*” Balletto & Passerin d'Entrèves, 1986. — *Boll. Mus. reg. Sci. nat. Torino* 4 : 133, 135. — Subsequent misspelling of the name *Algirica* Oberthür, 1876 (see also Balletto, Toso & Lattes, 1989 : 151, 154, 155, 157, 158, 161, 170, 181, 184 and Balletto *et al.*, 1990 : 185, 189).

ILLUSTRATIONS. Plate 4, figs. 3–4. Plate 9, figs. 1–4 (androconial scales). Text fig. 14 (male genitalia). Text fig. 15 (female genitalia).

MATERIAL EXAMINED. Morocco, Middle Atlas : 79 ♂, 41 ♀ in colls. VLCA, ZMA ; Algeria, vic. Oran : 1 ♂, 3 ♀ in coll. ZMA ; Algeria, Aurès Mts. : 6 ♂, 7 ♀ in coll. VLCA.

DESCRIPTION. Forewing length : see table 1 ; slightly larger than *H. maderensis*. Male upperside ground-colour a warm medium brown, wing markings well developed, blackish brown spots in s2 and s5 on forewing and in s2 on hindwing always present and with a white pupil, those on forewing much enlarged ; forewing as a rule with a more or less continuous row of creamy yellow patches from s1b up to s5, usually interrupted in s4 and the upper half of s3, extending basad to the sex brand, making the males look much like the females (this was already noticed by Oberthür, 1876 in his description of the taxon on p. 27 : “Dans le mâle d’Algérie, les taches fauves clair des ailes en dessus sont aussi vivement marquées que dans la femelle de France” [i. e. *H. semele* ♀ from France]) ; sex brand more reduced than in *H. maderensis*, *H. aristaeus* and most *H. senthes*, in the cell along the median vein and extending distad into the basal part of s2–s3 and the adjoining upper part of s1b ; hindwing with complete series of small light orange-ochreous patches in s2–s5(6), that remain separated by the broad brown underlining of the veins and that do not extend much basad. Female similar to male, but markings more complete, creamy yellow to orange-ochreous, sometimes with a shading of the same colour in the discal area in s2(3), touching the cell basad. Underside with same general pattern as *H. maderensis*, hindwing lighter than in the latter species ; discal line in both sexes distinctly bending distally in s4–s5, always pointed. Male genitalia much like *H. maderensis*, but gnathos tends to be slightly shorter (though not constantly so), tegumen slightly more robust (HT 2 *H. algerica* > *H. maderensis*), valve usually shorter than in *H. maderensis*. Female genitalia overall size of sterigma generally slightly less than in *H. maderensis*, much as in superspecies *H. azorina*, dorso-lateral lobe and dorsal lamella usually smaller than in *H. maderensis*, but there is overlap ; corpus bursae as a rule smaller than in *H. maderensis* and *H. aristaeus*, signum slightly shorter. Androconial scales as in *H. maderensis*, perhaps a little more slender (plate 9).

DISTRIBUTION. Widespread in hilly or mountainous areas in the Maghreb states, from the High Atlas (Tizi-n-Test, Amizmiz, Ourika, Tizi-n-Tichka, Djebel Ayachi, Tizi-n-Talrhemt,...), the Middle Atlas (Col du Zad, Tizi Tarhzeft, Foum Kheneg, Timahdite, Djebel Hebri, Azrou, Mischliften, Tizi-n-Tretten, Ifrane, Ras-el-Ma–Cèdre Gouraud, Imouzzèr-du-Kandar, Annoceur, Sefrou,...) and the Rif mountains

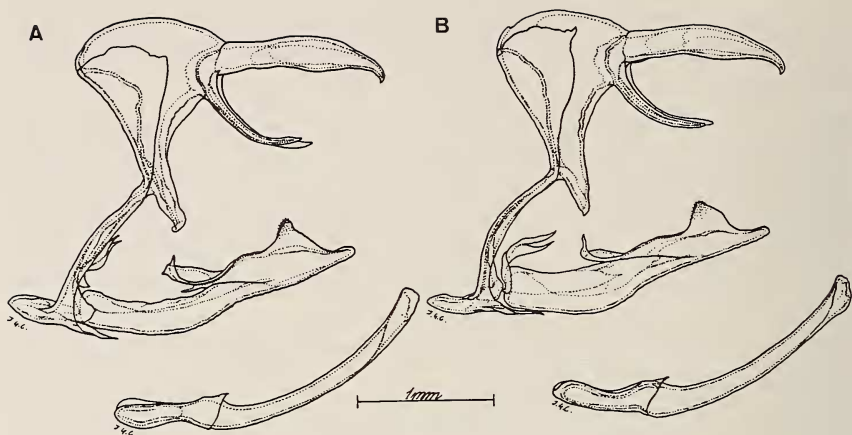


Fig. 14. *Hipparchia algerica* (Oberthür, 1876) : male genitalia.
 A. Morocco, Middle Atlas, Tizi-n-Tretten (1950 m), 22.VI.1994, leg. A. Olivier, in coll. VLCA (Prep. JGC no. 2524). B. same data as A (Prep. JGC no. 2525).

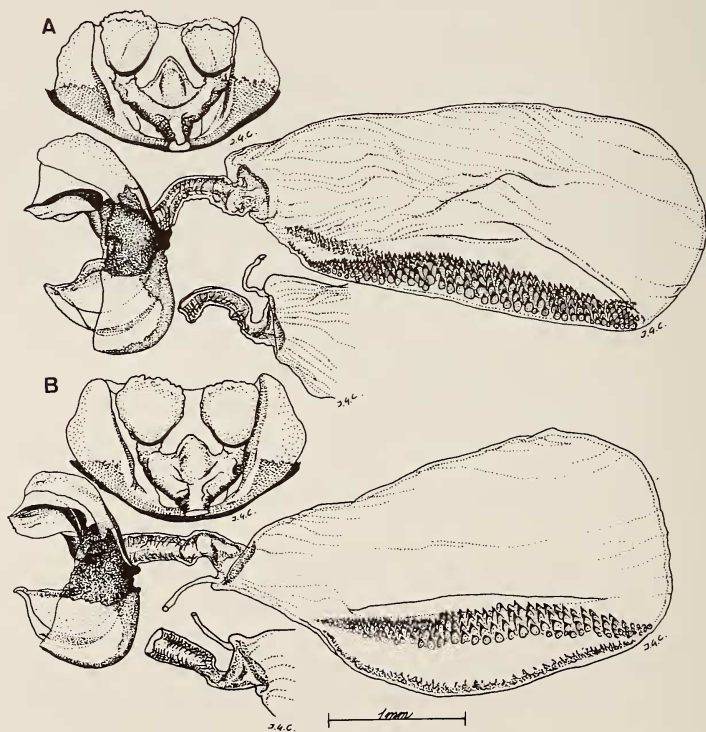


Fig. 15. *Hipparchia algerica* (Oberthür, 1876) : female genitalia.
 A. Morocco, Middle Atlas, Tizi-n-Tretten (1950 m), 27.VI.1994, leg. A. Olivier, in coll. VLCA (Prep. JGC no. 2528). B. same data as A (Prep. JGC no. 2530).

(Djebel Tidirhine,...) in Morocco, over the High Plateaux (Magenta, Sebdou, Teniet-el-Amar, El Bayadh [formerly Géryville], Djebel Ksel, Stite, Oran, Mascara, Djelfa, Aflou), the Tell Atlas (Col de Chréa, Daya, Teniet-el-Had) via the region of Algiers (Hussein Day, Blida, Blida-les-Glacières, Guelt-es-Stel) and Kabylie (Grande Kabylie, Yakouren, Djurdjura Massif) eastwards till Collo and the Aurès mountains (Khenchela, El Kantara, Lambessa, S'Gag, Djebel Chelia, Batna,...) in Algeria, reaching Tunisia (Djebel Chambi, Djebel Semmama, etc.) (sources : Oberthür, 1876, 1909, 1914, 1922 ; Fontaine, 1906 ; Meade-Waldo, 1906 ; Powell, 1914 ; Rothschild, 1914, 1917, 1925a, 1925b, 1929 ; Korb, 1916 ; Faroult, 1917 ; Cros & Dupont, 1927 ; Fison, 1931–1932 ; Zerny, 1935 ; Chnéour, 1939, 1942, 1947–1948, 1954, 1963 ; Wagener, 1952 ; Barragué, 1954, 1961 ; Varin, 1959 ; Roell, 1963 ; Wyatt, 1968 ; de Worms, 1969, 1973 ; de Freina, 1975 ; Schuurmans, 1976 ; Kudrna, 1977 ; Schmidt-Koehl, 1978, 1981 ; de Bros & Schmidt-Koehl, 1979 ; Devarenne, 1981, 1990 ; Coutsis, 1984 ; Tennent, 1988, 1993, 1995, 1996a, 1996b ; TARRIER, 1996a, 1996b, 1997). Once collected on Malta (Jutzeler *et al.*, 1997).

BIONOMICS. The preferred habitat seems to be open *Quercus ilex* L. woodland with clearings, that contain abundant nectar sources, principally thyme (*Thymus*) and thistles (? *Carduus*), generally at altitudes from 1000 m to well over 2000 m, sometimes as high as 2600 m (Tennent, 1995 reports it on one occasion from an altitude of 2788 m on the Adrar-n-Guinous, the highest peak above the Tizi-n-Test, at the western end of the High Atlas in Morocco), but occasionally much lower down, e. g. in El Kantara (Aurès mountains, E. Algeria) at 550 m (Powell, 1914 ; Wagener, 1952 ; Varin, 1959 ; Schuurmans, 1976 ; Thomas & Mallorie, 1985b ; TARRIER, 1996a, 1996b). In early summer (June) the butterfly visits flowers (Powell, 1914 ; Varin, 1959 ; Barragué, 1961), later (July–September), when habitats become barren (cf. Tennent, 1996b), the butterfly hides in bushes of *Quercus ilex* or sits on tree trunks, great numbers flying out of the bushes when disturbed (Powell, 1914). It has been noticed on *Cedrus* trunks as well (Varin, 1959) and there is one report of butterflies sitting on animal excrements (Oberthür, 1922). Powell (1914) also encountered *H. algerica* in uncultivated plains and on arid mountains and hills : in such treeless areas it settles on the ground or on rocks, often within the shade of a grass tussock. Barragué (1954) also notes that it settles exclusively on the ground. One of us (AO) observed the butterfly between 21 and 28.VI.1994 in several localities of the Middle Atlas in Morocco. They were mostly sitting on *Quercus ilex* trunks and branches at Ifrane (1650 m) and on the Tizi-n-Tretten (1950 m), a few on *Cedrus atlantica*

trunks in the area of Ras-el-Ma-Cèdre Gouraud. No nectar taking behaviour was noticed. On the Col du Zad (2100–2350 m), butterflies were sitting on stones and rocks and on the ground. Larval host-plants : several Poaceae species, most probably including *Lyngeum spartum* (Powell, 1914). Univoltine : observations covering all months from May to October (Powell, 1914 ; Rothschild, 1914, 1917 ; Faroult, 1917 ; Chnéour, 1942, 1947–1948, 1954 ; Mokhlès, 1984 ; Tennent, 1993), a few literary sources mentioning April as well (Higgins & Riley, 1970 ; Schuurmans, 1976 ; Kudrna, 1977 ; Rungs, 1981 ; Devarenne, 1990 ; Tolman & Lewington, 1997). This extended flight period has led some authors to believe that two broods are involved (Chnéour, 1942, 1954 ; Devarenne, 1981, 1990 ; Tennent, 1996b), a statement that certainly is not correct. Most probably the butterflies emerge in early summer (May–June) and aestivate from late June until late August, as suggested by their midsummer behaviour (cf. Powell, 1914 ; Tennent, 1993 ; Tarrier, 1996a ; Tolman & Lewington, 1997). Powell (1914) remarks that, at the end of August and in September, the male, that thus far seemed indifferent to the female, starts courting her. Females were induced by Powell to lay eggs in captivity : they never oviposited in June and July, starting only during the last days of August and, more easily, in September. This suggests a mechanism of photoperiodically controlled delayed ovarian maturation well known in several satyrine butterflies, including *H. semele* in central Spain (cf. García-Barros, 1988). Early stages : no description, but Powell (1914) presents some notes on larval behaviour. The larva grows slowly during winter ; when temperatures are not too low it feeds continuously. Pupation takes place underground in May. At Aflou (High Plateaux, Algeria), he found a few larvae under stones contiguous to tussocks of *Lyngeum spartum* during the day (15.V.1911) ; they were almost full grown and soon pupated. Several caterpillars were collected at night on the hills and mountains near Lambessa (Aurès mountains, E. Algeria) in May 1913, sitting on top of the leaves of several Poaceae species while feeding.

COMMENTS. This taxon was described as a “varietas” [= subspecies] of “*Satyrus Semele* L.” by Oberthür (1876), and subsequently considered as such (or sometimes as “race”) by all authors for nearly seventy-five years (Kirby, 1877 ; Lang, 1884 ; Heyne, 1895 ; Tutt, 1896 ; Staudinger & Rebel, 1901 ; Fontaine, 1906 ; Spuler, 1908 ; Oberthür, 1909, 1914, 1922 ; Powell, 1914 ; Rothschild, 1914, 1917, 1925a, 1925b, 1929 ; Stauder, 1915–1916 ; Korb, 1916 ; Rebel, 1916 ; Faroult, 1917 ; Verity, 1923–1924, 1938–1939, 1953b (as a “race” of “*exerge*” *aristaeus* in the latter publication) ; Cros & Dupont, 1927 ; Gaede, 1930, 1931 ;

Fison, 1931–1932 ; Zerny, 1935 ; Chnéour, 1939, 1942, 1947–1948) and, more recently, Wyatt (1956, 1968), Roell (1963) and de Toulgoët (1966), while Meade-Waldo (1906), Seitz (1908) and Barragué (1954) simply list it as “*Satyrus semele*”. Verity (1923) described race *pallidalgirica* of *Hipparchia semele* from Lambessa and Blida. This taxon was recognized by Gaede (1930), Chnéour (1942), de Lattin (1949), Verity (1953b), Varin (1960) and Leestmans (1965, 1968). Kudrna (1977) synonymized it under nominotypical *H. algerica*, a decision fully supported both by the lack of differentiation of any Algerian population and by the fact that the lectotype of *algerica* and the syntypes of *pallidalgirica* originate from the same locality ! In his revision of the “*Hipparchia semele* Gruppe”, de Lattin (1949) treated *algerica* as a “Rasse” [= subspecies] of *Hipparchia aristaetus*, in which he was followed by Varin (1960), Leestmans (1965, 1968), Higgins & Riley (1970, 1984), de Freina (1975), Zangheri (1975), Higgins (1975), Schuurmans (1976), Devarenne (1981, 1990), Higgins & Hargreaves (1983), Coutsis (1984), Vassilaina-Alexopoulou & Mourikis (1985), Thomas & Mallorie (1985b), Tennent (1993, 1996a, 1996b, 1997), TARRIER (1995a, 1996a, 1997) and Tolman & Lewington (1997), while some authors just report it as *Hipparchia aristaetus* (Bernardi, 1961 ; de Worms, 1969, 1973 ; Thomas & Mallorie, 1985a ; TARRIER, 1995b, 1996b and Tennent, 1995). Finally, *H. algerica* is listed as a species in its own right by de Lesse (1951, 1952), de Lattin (1952), WAGENER (1952), Chnéour (1954, 1955, 1963), Varin (1959), Barragué (1961), Valletta (1972), Kudrna (1975, 1976, 1977, 1984), Varga (1977), Schmidt-Koehl (1978, 1981), de Bros & Schmidt-Koehl (1979), Battenfeld (1979), Rungs (1981), Koçak (1981–1983), Bivar de Sousa (1982a, 1985a, 1986), Mokhlès (1984), Balletto & Passerin d’Entrèves (1986), Tennent (1988), García-Barros (1988), Taymans (1989), Balletto *et al.* (1990), D’Abrera (1992), Meyer (1993), Cesaroni *et al.* (1994), Balletto (1995) and Jutzeler *et al.* (1997). We treat it as a full species because of its total geographical isolation, distinct habitat specialization, differentiated external phenotype and allozyme differentiation (the data by Cesaroni *et al.*, 1994 in this last respect convincingly support the full species status of *H. algerica*).

5.3. *Hipparchia aristaetus* (Bonelli, 1826)

“*Papilio Satyrus Aristaetus*. Bon.” Bonelli, 1826. — *Memorie Accad. Sci. Torino* 30 : 177–179, Tav. II, Fig. 1. ♂, Fig. 1. ♀. Locus typicus : Sardinia, monte Genargentu [Monti del Gennargentu], 800–1000 m. Type material : lectotype ♂, paralectotypes 1 ♂, 2 ♀,

- in Museo zoologico della Università di Torino ; design. Balletto & Passerin d'Entrèves (1986 : 135).
- “*Satyrus Aristaeus*” Bonelli in Desmarest, 1825. — *Bull. Sci. nat. Géol.* (2) 4 : 249. Locus typicus : Sardinia. — Unavailable name (Article 12(a) of ICZN). Nomen nudum (Balletto & Passerin d'Entrèves, 1986 : 134 (135)).
- “*Satyrus Aristeus*” Rambur, 1832. — *Annl. Soc. ent. Fr.* 1 : 252, 262 — Subsequent misspelling of the name *Aristaeus* Bonelli, 1826 (see also Rambur, 1833 : 53 ; Ghiliani, 1852 : 143 ; Sheldon, 1907 : 77 ; Varin, 1960 : 13, 16, 17 ; Fonteneau, 1962 : 228 ; Stempffer, 1962 : 266 ; Leestmans, 1965 : 24, 89, 92, 94, 114, 182, 184, 185, 1966 : 195, 1968 : 303, 351 ; de Granville, 1968 : 209 ; Schmidt-Koehl, 1975 : 54 ; de Bros & Schmidt-Koehl, 1979 : 15 ; Sammut, 1984 : 47, 111 ; Bivar de Sousa, 1986 : 49–50 ; Smith & Shreeve, 1990 : 275, 276, 277 ; Prola & Prola, 1990 : 45 ; Littler, 1991 : 27 and Dennis, Williams & Shreeve, 1991 : 46).
- “*Sátyrus sémele* L. v. *sardóá*” Spuler, [1902]. — Die Schmetterlinge Europas. I. Band. Allgemeiner Teil — Spezieller Teil. Rhopalocera. Hesperidae. Sphingidae. Notodontidae. Thaumtopoeidae. Drepanidae. Saturniidae. Lemoniidae. Endromidae. Lasiocampidae. Lymantriidae. Noctuidae. Cymatophoridae und Brepthidae : 43. Locus typicus restrictus : Sardinia, Lago Alto del Flumendosa, ca. 1000 m (Kudrna, 1977 : 112). Type material : neotype ♂, in Landessammlungen für Naturkunde, Karlsruhe ; design. Kudrna (1977 : 112). — Junior subjective synonym of *Papilio Satyrus Aristaeus* Bonelli, 1826 (Verity, 1953b : 308, 310 ; Bernardi, 1961 : 198 ; Kudrna, 1984 : 237).
- “*Satyrus Semele* var. nov. *Rautheri* m.” Krausse-Heldrungen, 1912. — *Arch. Naturgesch.* 78A (9) : 159. Locus typicus : Sardinia, Monti del Gennargentu, “Sedda de Pranu”. Type material : unknown. — Junior subjective synonym of *Papilio Satyrus Aristaeus* Bonelli, 1826. Infrasubspecific taxon (Hemming, 1931 : 502 ; Bytinski-Salz, 1934 : 92 ; Verity, 1953b : 307, 310 ; Kudrna, 1977 : 110).
- “*Satyrus semele aristaens*” Gaede, 1930. — Satyridae [part.]. In : Seitz, A. (Ed.) : Die Gross-Schmetterlinge der Erde. Eine systematische Bearbeitung der bis jetzt bekannten Gross-Schmetterlinge I. Supplement 1 : 163. — Subsequent misspelling of the name *Aristaeus* Bonelli, 1826 (see also Robinson, 1971 : 679 and Bernardi, 1971 : 31).
- “*Hipparchia semele*, Linn. ssp. *ichnusa*, nom. nov. pro *Papilio aristaeus*, Bonelli” Hemming, 1931. — *Trans. ent. Soc. London* 79 : 502.

— Junior objective synonym of *Papilio Satyrus Aristaeus* Bonelli, 1826 (Kudrna, 1984 : 237 ; Balletto & Passerin d'Entrèves, 1986 : 135) and junior subjective synonym of *Sátyrus sémele* L. v. *sardóá* Spuler, [1902] (Verity, 1953b : 308–309 ; Kudrna, 1977 : 110).

“*Satyrus semele* L. var. *aristaeus* Bon. ab. n. *postcaeca* m.” Schawerda, 1931. — *Z. öst. EntVer.* 16 : 31. Locus typicus : Corsica, Evisa. Type material : unknown. — Junior subjective synonym of *Papilio Satyrus Aristaeus* Bonelli, 1826. Infrasubspecific taxon (Kudrna, 1977 : 113).

“*Hipparchia ariseus*” Smith & Shreeve, 1990. — *Entomologist's Rec. J. Var.* 102 : 277. — Subsequent misspelling of the name *Aristaeus* Bonelli, 1826.

“*Hipparchia aristhaeus senthes*” Cuvelier & Spruytte, 1994. — *Bull. Cercle Lépidopt. Belg.* 23 : 117. — Subsequent misspelling of the name *Aristaeus* Bonelli, 1826.

ILLUSTRATIONS. Plate 4, figs. 5–6. Plate 10, figs. 1–4 (androconial scales). Text figs. 16–17 (male genitalia). Text fig. 18 (female genitalia).

MATERIAL EXAMINED. Italy, Sardinia : 150 ♂, 44 ♀ in colls. VLCA, ZMA ; France, Corsica : 48 ♂, 14 ♀ in colls. VLCA, ZMA ; Italy, Elba : 4 ♂, 6 ♀ in colls. VLCA, ZMA.

DESCRIPTION. Forewing length : see table 1 ; slightly smaller than *H. algirica*, but larger than *H. maderensis* (except for the Corsica females, but $n = 14!$). Male upperside ground-colour as in *H. algirica*, blackish brown spot in s2 on forewing small to minute, often without white pupil ; markings on forewing variably expressed, from entirely absent except for vestigial orange patches distad of spots in s2 and s5, to a more or less continuous orange-ochreous band from s1b up to s5, of a warmer, more reddish tinge and much wider than in *H. algirica*, filling the entire space except for the marginal area, basad till the sex brand ; sex brand much more extended than in *H. algirica*, quite as in *H. maderensis* ; hindwing with complete series of warm orange to reddish orange patches in s2–s6, usually filling the entire space except for the marginal area, extending basad almost until the cell, forming a continuous band only interrupted by thin, though well marked, brown veins, in the least marked specimens not extending beyond s5, which last space is then only barely coloured so distally. Female with markings much more complete, forewing moreover often with a shading of the same colour in the discal area in s1b–s3, sometimes even invading the cell, patches on hindwing always reaching s6. Underside forewing in both sexes entirely warm orange, except along costa, apex and outer margin, contrast between more vividly coloured basal-discal area and

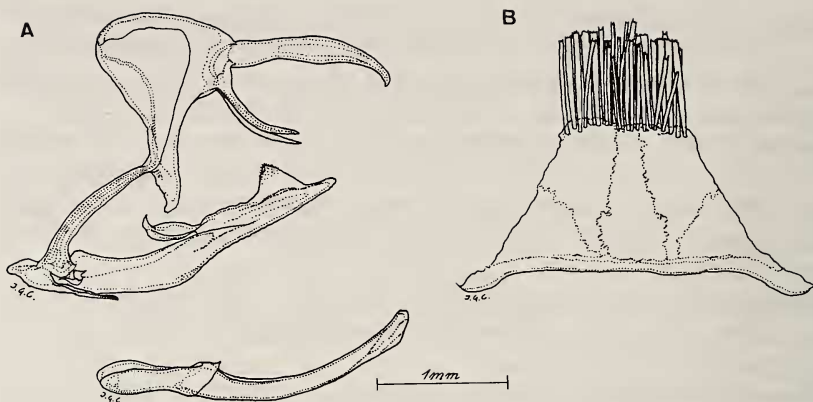


Fig. 16. *Hipparchia aristaeus* (Bonelli, 1826): male genitalia (A) and Jullien organ (B).

Italy, Sardinia, Prov. Nuoro, Monti del Gennargentu, 4 km S. Fonni (1000 m), 22.VII.1992, leg. A. Olivier, in coll. VLCA (Prep. JGC no. 2274).

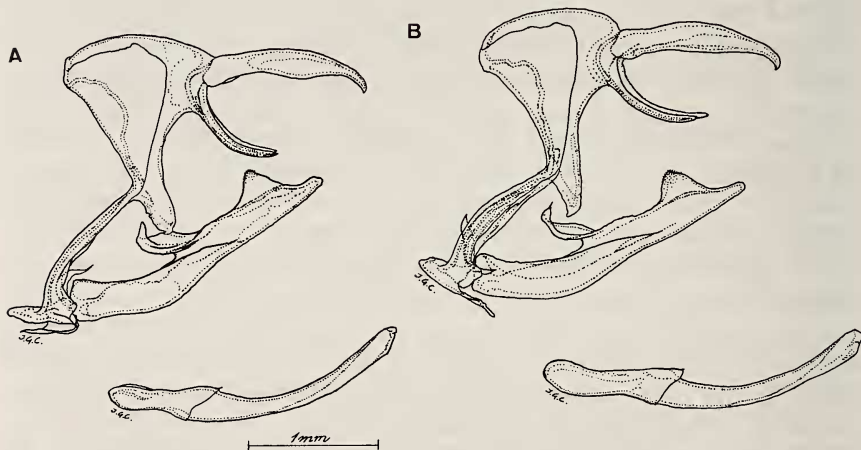


Fig. 17. *Hipparchia aristaeus* (Bonelli, 1826): male genitalia.

A. Italy, Sardinia, Prov. Nuoro, Monti del Gennargentu, 4 km S. Fonni (1000 m), 24.VII.1992, leg. A. Olivier, in coll. VLCA (Prep. JGC no. 2273). B. Italy, Elba, Mt. Le Calanche (approx. 800 m), 9.VII.1988, leg. C. Warnotte, in coll. VLCA (Prep. JGC no. 2270).

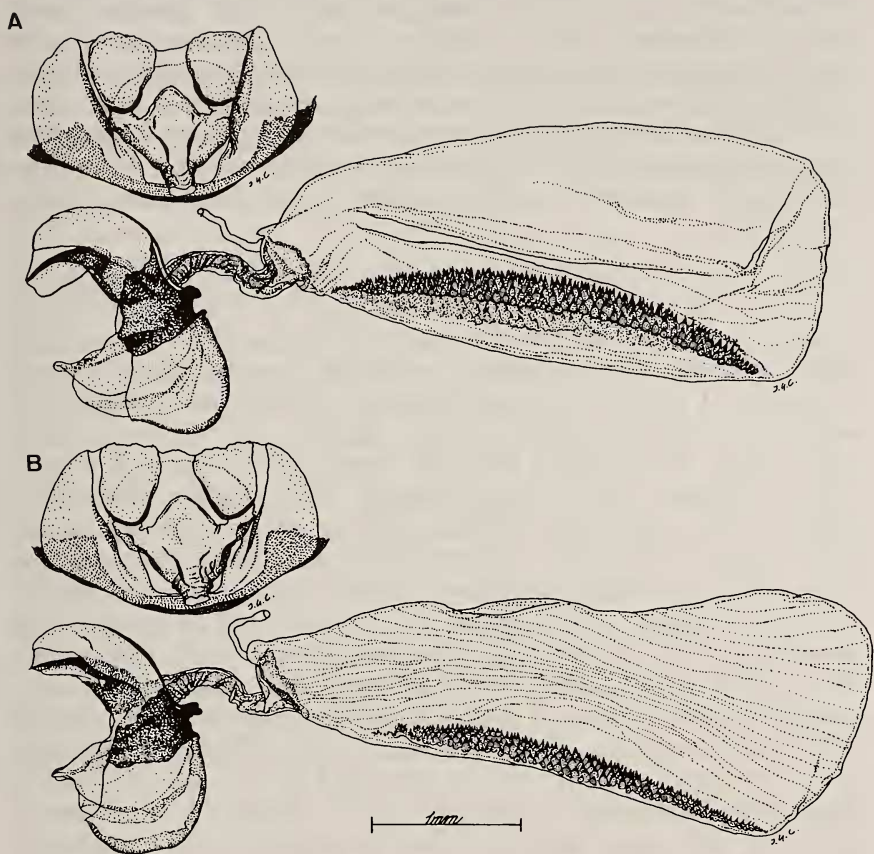


Fig. 18. *Hipparchia aristaeus* (Bonelli, 1826) : female genitalia.

A. Italy, Sardinia, Prov. Nuoro, Monti del Gennargentu, 4 km S. Fonni (1000 m), 22.VII.1992, leg. A. Olivier, in coll. VLCA (Prep. JGC no. 2462). B. France, Corsica, Haute-Corse, Calvi, 13/27.VII.1971, leg. Fam. van Oorschot & Fam. Coene, in coll. VLCA (Prep. JGC no. 2464).

lighter postdiscal area far less pronounced than in other species of this group, except for some extreme specimens of Sicilian *H. senthes*; spot in s2 often absent in male. Underside hindwing discal line gently bending distally in s4–s5, evenly rounded in male, usually more pointed but sometimes also evenly rounded in female. Male genitalia much like *H. maderensis* and *H. algerica*: uncus, vinculum and valve sometimes longer than in these species, but there is overlap. Female genitalia sterigma much like *H. maderensis*, corpus bursae larger than in *H. algerica*, signum slightly longer. Androconial scales longer than in *H. (azorina) azorina*, *H. maderensis*, *H. algerica* and most *H. senthes*, much like *H. (azorina) miguelensis* (plate 10, see also Kudrna, 1984: 236, fig. 10).

DISTRIBUTION. Sardinia (known from the central and eastern part of the island: Monti del Gennargentu, Barbágia Seulo, Barbágia Ollolai, Lanusei, Ogliastra; recently also found in the north: Porto Tórres, Monte Limbara, Témpio Pausánia, as well as the small offshore island of Asinara); Corsica (widespread over most of the island); Elba (rather widespread); Giglio; Capraia (sources: Bonelli, 1826; Calberla, 1887; Verity, 1908, 1917, 1953b; Rocci & Turati, 1925; Hartig & Amsel, 1951; Leestmans, 1965; Schmidt-Koehl, 1975; Hartig, 1975–1976; Kudrna, 1977; Biermann & Hesch, 1982a, 1982b; Cesaroni *et al.*, 1994; Terzani, 1995, etc.). This species has erroneously been reported from other areas as well, either as a result of a more inclusive species concept, in which i. e. *H. algerica*, *H. "blachieri"* and *H. senthes* were assimilated under *H. aristaeus* (examples include North Africa (vide supra), Sicily (Costa, 1840; von Kalchberg, 1872; Lang, 1884, illustrating a Sicilian *H. senthes* female as *aristaeus*; Heyne, 1895; Sichel, 1962, 1963; Bretherton, 1966; Higgins & Riley, 1970 (p. 141: "A large race, f. *siciliana* Oberthur (...) occurs in the Lipari Islands, Sicily (Mt. Etna region) and Giglio"); Zangheri, 1975; Bigger, 1977; D'Abbrera, 1992, also illustrating Sicilian *H. senthes* specimens as *H. aristaeus* on p. 203; Cernigliaro, Di Benedetto & Lombardo, 1994), S. Italy (Higgins & Riley, 1970; Zangheri, 1975; D'Abbrera, 1992), Malta (Bretherton, 1966) as well as the Balkans, including Greece with the Aegean islands, and Turkey (de Lesse, 1960; Bernardi, 1961; Sichel, 1962; Stempffer, 1962; Higgins, 1966; Bretherton, 1968, 1970; Coutsis, 1969, 1972, 1985a, 1985b, 1992, 1994; Robinson, 1971, 1990; de Worms, 1972; Koutsaftikis, 1974a, 1974b, 1974c; Bigger, 1974; Cribb, 1974; Schaidler & Jakšić, 1989 (on p. 74–75); Gaskin & Littler, 1993; Withrington, 1995; Pamperis, 1997, who makes the following curious statement (p. 333): "There is great confusion about the names used for these species, because several other names had been used in

the past, such as (...) *algerica* and *senthes* instead of *aristaeus*") or due to misidentifications (one such instance is the series of reports from the Lipari Islands by Sichel, 1962; Higgins & Riley, 1970, 1984; Higgins, 1975 and Zangheri, 1975, that all apply in fact to *H. leighebi*). Quite recently, Tolman & Lewington (1997) erroneously reported it from Ponza, an island from where only *H. sbordonii* is known (these authors do not mention that taxon at all in their book). Heyne (1895) also mentions it from "Wiesbaden (in heissen Jahren)", suggesting that *aristaeus* is only a climatic form and Vorbrodtt (1911) cites it as "Angeblich aus dem Wallis von Berisal (Favre)", presumably on similar grounds. Both last records evidently apply to *H. semele*. Verity (1911 : 313) describes "*Satyrus Aristaeus* Esp. race *variegata*" from Lardy near Paris, Pont-de-l'Arche and Authion. Obviously, this is a junior subjective synonym of *Papilio Semele* Linnaeus, 1758.

BIONOMICS. *H. aristaeus* has been observed in a variety of, mostly xeric, habitats, varying from dry rocky hills and garrigue (Verity, 1908, 1917; Hartig, 1975–1976; Kudrna, 1977; Biermann & Hesch, 1982a) and maquis with a. o. *Arbutus unedo* L. and *Erica arborea* L. (Bigot, 1959; Leestmans, 1965; Balletto, Toso & Lattes, 1989) to various stages of woodland (Bigot, 1959; Balletto, Toso & Lattes, 1989). Bytinski-Salz (1934) found it "in duncklen Waldesinnern" in mixed deciduous woodland (*Castanea sativa* Mill., *Corylus avellana* L., *Juglans regia* L.), while on Corsica it has even been recorded on humid alpine grassland up to the screes of the Monte d'Oro (Bigot, 1959). Last-mentioned author reviews the biocoenoses of Corsica and reports *H. aristaeus* (as "*Hipparchia algerica* Obth.?!") from most of these. See Balletto, Toso & Lattes (1989) for data on Sardinia and Elba. On Corsica, *H. aristaeus* has occasionally been reported from sea level (Schmidt-Koehl, 1975; Rungs, 1982; Owen, 1986), but it usually occurs in mountainous areas from 500 m up to well over 1500 m (Bigot, 1959; Fonteneau, 1962; Leestmans, 1965; Schmidt-Koehl, 1975; Rungs, 1982). From Sardinia, the great majority of the literature records are from altitudes between 800 m (Bonelli, 1826) and about 1600 m (Hartig, 1975–1976), though Cesaroni *et al.* (1994) found it at some lowland localities near sea level in the north of the island and at 150 m on Asinara. One of us (AO) observed the butterfly between 19 and 25.VII.1992 in several localities in the central part of Sardinia (province of Nuoro). On 19.VII, one single male was taken 3 km W. Seui (Barbàgia Seulo) at an altitude of only 400 m. On 22.VII, numerous freshly emerged males and only one female were noticed 12 km SE. Fonni (Monti del Gennargentu) at 500 m on dry garrigue with low bushes of *Quercus* sp. Most observations, however, were made daily

from 21 to 25.VII on a habitat 4 km S. Fonni (Monti del Gennargentu) at 1000 m, at the beginning of emergence. Males were clearly outnumbering females, but after about two days the latter became progressively commoner. The main habitat consisted of rough, open ground with low vegetation, with the males perching on the ground or on rocks, flying actively towards any potential mate, the females only occasionally flying along. Females were encountered more often, especially on the last day of recording, among the undergrowth at a nearby woodland edge or, sometimes, sitting on *Rubus* sp. bushes. This suggests a partial habitat segregation between sexes, the females visiting male leks only for mating, a situation also reported for *H. leighebi* (Kudrna & Leigheb, 1988), *H. sbordonii* (Kudrna & Leigheb, 1988 ; Olivier, pers. obs. July 1991 on Ponza) and *H. maderensis* (vide supra). On Elba, the butterfly is found at low elevations (Verity, 1908) up to about 800 m (C. Warnotte, pers. comm.). On Giglio, Biermann & Hesch (1982a) found it "sehr häufig in Felsbereichen der Insel [very common in rocky areas of the island]" and Cesaroni *et al.* (1994) encountered it there at Giglio Castello (Grosseto), at an altitude of 500 m. On Capraia, one single male was found at Il Laghetto (318 m) on 4.VII.1994 (Terzani, 1995). The butterfly is often observed taking nectar : AO saw it occasionally on an unidentified low plant with blue flowers, females also on *Rubus* sp. (Rosaceae). Fonteneau (1962) and Jutzeler, Pitzalis & de Bros (1995) both mention *Carlina corymbosa* L. (Asteraceae) as the preferred nectar source of *H. aristaeus*, while Owen (1986) lists *Inula viscosa* (L.) Aiton (Asteraceae), *Mentha aquatica* L. and *Mentha ?suaveolens* Ehrh. (Lamiaceae). Larval host-plants : various Poaceae. Jutzeler, Pitzalis & de Bros (1995) mention the Sardinian endemics *Festuca morisiana* and *Poa balbisii* as predominating species in the habitat where *H. aristaeus* was observed. Rearing in captivity was successful on both forementioned grass species, as well as on *Brachypodium ramosum* (from S. Italy), *Festuca ovina*, *Festuca rubra* (both from Switzerland) and *Festuca* sp. (from near Genoa, N. Italy). Leestmans (1965) lists "*Aira canescens*, *Triticum repens*, les *Brachypodium*, *Festuca*, *Poa* et autres Graminées", which are exactly the species listed — in the same order — by Verity (1953b) as larval host-plants of *H. semele* ! Univoltine : on Corsica from the last week of June (Fontaine, 1907 ; Schmidt-Koehl, 1975 ; Verdonck, 1996) till October (Rungs, 1982 ; F. Coenen, pers. comm. : the latter found very worn specimens of both sexes on 2–8.X.1988). On Sardinia the flight period usually starts only at about mid-July (Hartig, 1975–1976 ; Biermann & Hesch, 1982b) or, on the Monti del Gennargentu, even late July (Hartig, 1975–1976 ; Olivier, pers. obs. 1992), but the butterfly is recorded there as early as 30.VI.1994 by Jutzeler, Pitzalis & de Bros (1995 : "nombre d'*aristaeus* mâles") ;

starting on 5.VII.1975 at Lanusei (Biermann & Hesch, 1992b). It flies until at least the end of August (Hartig & Amsel, 1951; Hartig, 1975–1976) and in coll. ZMA there are some worn specimens collected as late as 30.IX–6.X.1957 (leg. C. A. Jeekel), while Cesaroni *et al.* (1994) still found it on 12.X.1989 at Porto Tórres on the northern coast. From Elba there are reports covering a period from 20.VI to 8.X (Verity, 1917; Greenwood, 1964; Biermann & Hesch, 1982a: only worn females collected between 29.IX and 8.X.1980) and from Giglio we have precise data only from Biermann & Hesch (1982a: 3 & 4.VII.1979) and Cesaroni *et al.* (1994: 20.VIII.1989). Early stages: described in detail by Jutzeler, Pitzalis & de Bros (1995). According to these authors, females started egg-laying after only three days. Also in material from Corsica, the females started oviposition in captivity soon after being captured (Jutzeler *et al.*, 1997). Records of worn specimens of both sexes in September–October (vide supra) suggest, however, that aestivation of the adults may occur as well, especially in lowland localities with a more extreme mediterranean climate. From L2 on, the larvae feed only at night, without real diapause in winter.

COMMENTS. Up until quite recently, there has been a lot of confusion, both nomenclatural and taxonomic, around this species, resulting in an unfortunate series of misunderstandings. The name *Satyrus Aristaeus* was first introduced by Bonelli in Desmarest (1825), but as no formal description accompanied it, it is a nomen nudum (cf. Article 12(a) of ICZN). Subsequently, Bonelli (1826) validly described the taxon *Papilio Satyrus Aristaeus* from the “monte Genargentu” on Sardinia, while Hübner ([1826]) illustrated on Plate 68, figs. 32 to 35, specimens agreeing in every respect with this new taxon under the name *Papilio Semele*. With the notable exception of Herrich-Schäffer ([1844]), who reported on it as *Satyrus Aristaeus*, all subsequent early authors for over a century listed it as a “varietas” [= subspecies] (or sometimes “race”) of “*Satyrus Semele*” (Rambur, 1832: “Il n’est évidemment qu’une variété du *Semele* (L)”; Ghiliani, 1852; Lederer, 1858; Staudinger, 1870, 1871, 1879; Kirby, 1871, 1903; Lang, 1884; Calberla, 1887; Heyne, 1895; Tutt, 1896; Mathew, 1898; Fletcher, 1901; Staudinger & Rebel, 1901; Rebel, 1903, 1904, 1916; Rosa, 1905; Gurney, 1906, 1914; Sheldon, 1907; Fontaine, 1907; Verity, 1908, 1916, 1917, 1923–1924, 1938–1939, 1953a, 1953b: in both latter publications as “*Hipparchia (Hipparchia) semele* L. eserge *aristaeus* Bon. razza *aristaeus* Bon.”; Spuler, [1902]; Seitz, 1908; Oberthür, 1909, 1914; Vorbrodts, 1911; Krausse-Heldrunge, 1912; Stauder, 1915–1916; Ragusa, 1916–1919; Verity & Querci, 1922–1924; Bubaček, 1923; Rocci & Turati, 1925; Reisser & Kautz, 1927; Schawerda, 1927,

1931 ; Warnecke, 1928 ; Gaede, 1930 ; Hemming, 1931 ; Bytinski-Salz, 1934 ; Holik, 1949). Spuler ([1902]), apparently not having consulted Bonelli's original description, wrongly assumed that the type locality of "*Sátyrus semele* L. v. *aristaëus* Bon." was "Corsica (und Elba?)", and, considering the Sardinian population to be distinct, erected the new name "*Sátyrus semele* L. v. *sardóa*" for the latter. This mistake about the type locality of *H. aristaëus* was subsequently perpetuated by Gaede (1930), Holik (1949), de Lattin (1949, 1967), Varin (1960) and Leestmans (1965, 1968). Hemming (1931) created additional confusion making the following statement (p. 502): "This subspecies of *Hipparchia semele*, Linn. (1758), was described in 1826 by Bonelli as *Papilio aristaëus*. The latter name is invalid as it is a primary homonym of *Papilio aristeus*, Stoll (1780 in Cramer, *Uitl. Kapellen*, 4(27): 60) and of *Papilio aristeus*, Stoll (1781, *ibid.*, 4(31): 139). I therefore propose the name *Hipparchia semele*, Linn. ssp. **ichnusa***, **nom.nov.** pro *Papilio aristaëus*, Bonelli". In doing so, Hemming (l. c.) made two mistakes: firstly, if the primary homonymy established by this author had been justified, Spuler's name *sardoa* was already available and both Verity (1953b) and Kudrna (1977) consequently correctly synonymized *ichnusa* under that name (only Biermann & Hesch, 1982a, 1982b since then have used the name *ichnusa*), secondly, following Article 58 of ICZN, both names listed as primary homonyms by Hemming (1931) are not, as they have a different origin and meaning (cf. Tremewan, 1978 ; Holloway & Robinson, 1979 ; Kudrna, 1984 ; Balletto & Passerin d'Entrèves, 1986 ; Hesselbarth, van Oorschot & Wagener, 1995). Stoll's *aristeus* could mean "a prince" (Tremewan, 1978), "the best, often used as a form of a title" (Kudrna, 1984), "un cavaliere greco [a Greek knight or horseman]" (Balletto & Passerin d'Entrèves, 1986) or it could be derived either from Aristeas, a wonder-worker and poet, or from Aristeas, son of Adeimantos (Hesselbarth, van Oorschot & Wagener, 1995). Bonelli's *aristaëus* undoubtedly applies to an epithet of Apollo (Tremewan, 1978 ; Kudrna, 1984 ; Balletto & Passerin d'Entrèves, 1986: "In una nota manoscritta Bonelli indica che il suo *aristaëus* deriva da uno degli epiteti di Apollo"), although Hesselbarth, van Oorschot & Wagener (1995) state that it is derived from Aristaios, son of Apollo and the Nymph Kyrene, king of Arcadia, who introduced the apiculture and the olive culture. Therefore, the possible ambiguity about the original generic combination, discussed by e. g. Balletto & Passerin d'Entrèves (1986) becomes superfluous and irrelevant for the present case. By now there apparently is a consensus of opinion on at least the different origin and meaning of the names *aristeus* and *aristaëus* and hence we fully agree with Tremewan (1978),

Holloway & Robinson (1979) and Balletto & Passerin d'Entrèves (1986) that, in the interest of stability [and in compliance with Article 58 of ICZN], the name *Hipparchia aristaeus* should be retained for this species. After Hemming (1931), it was Kudrna (1975) who again drew attention to the supposed case of homonymy between the two names and, considering *H. aristaeus* — as viewed in the present study — conspecific with North African *algirica*, used the latter name for it, and subsequently Higgins (1976) established *Hipparchia algirica sardoa* Spuler, [1902] as the “valid” name for the taxon from Sardinia and Corsica (a combination already used previously and for the first time by de Lattin, 1967). This combination, understood in the same sense as well, was subsequently used by Kudrna (1977), Leraut (1980), Rungs (1982), Fonteneau (1985) and Reinhardt (1992). Fonteneau (1962) presented the combination “*Hipparchia algirica aristaeus* [sic!]”, which is senseless, as Oberthür's name was published much later than both Stoll's and Bonelli's names. The “broad” species concept repeatedly used for the *Hipparchia aristaeus* group has resulted in some entries in the literature of “*algirica*” as the species name for *H. aristaeus* as understood here (e. g. Bigot, 1959 ; Johnson, 1963). The name *rautheri* was introduced by Krausse-Heldrunge (1912) as a “var.”, though from his very description one may deduce that he himself considered it to be an individual form. Subsequently, it was used as a valid “subspecific” name by Gaede (1930), Varin (1960) and Leestmans (1965). After Bonelli (1825, 1826) and Herrich-Schäffer ([1844]), it was de Lattin (1949) who finally established the distinct species status of *Hipparchia aristaeus* and, after him, *H. aristaeus* has been listed as a species in its own right — and under its correct name! — by de Lattin (1950), Hartig & Amsel (1951), Varin (1960), Bernardi (1961 (also as super-species, vide supra), 1971), Stempffer (1962), Sichel (1962), Bretherton & de Worms (1963), Greenwood (1964), Leestmans (1965, 1966, 1968, 1975), Bretherton (1966), de Granville (1968), Janse (1969), Kostrowicki (1969), Higgins & Riley (1970, 1984), Higgins (1973, 1975), Panchen & Panchen (1973), Schmidt-Koehl (1975), Zangheri (1975), Hartig (1975–1976), Roell (1977), Teobaldelli (1978), Tremewan (1978), Holloway & Robinson (1979), Heath (1981), Tennent (1983), Higgins & Hargreaves (1983), Coutsis (1984), Kudrna (1984, 1986, 1996), Balletto & Kudrna (1985), Balletto & Passerin d'Entrèves (1986), Bivar de Sousa (1986), Owen (1986), Kapfer (1987), Rungs (1988), Taymans (1989), Smith & Shreeve (1990), Prola & Prola (1990), Balletto *et al.* (1990), Dennis, Williams & Shreeve (1991), D'Abrera (1992), Cesaroni *et al.* (1994), Balletto (1995), TARRIER (1995b), Hesselbarth, van Oorschot & Wagener (1995), Terzani (1995), Jutzeler, Pitzalis & de Bros (1995),

Jutzeler, Grillo & de Bros (1995), Jutzeler, Biermann & de Bros (1996), Verdonck (1996), De Prins & Iversen (1996), Tolman & Lewington (1997), Jutzeler *et al.* (1997) and Dennis (1997). We treat it as a full species for the same reasons as we do with *H. algirica* (vide supra).

5.4. *Hipparchia semthes* (Fruhstorfer, 1908)

“*Eumenis (Satyrus) semele semthes* nova subsp. nov.” Fruhstorfer, 1908.

— *Int. ent. Z.* 2 : 10. Locus typicus : Taygetos [Greece, Pelopónissos, Óros Taígetos]. Type material : lectotype ♂, paralectotype ♀, in British Museum (Natural History), London [now The Natural History Museum, London] ; design. Kudrna (1977 : 116).

“*Satyrus Semele* L. ab. ♀ *Triocellatus* Ragusa” Ragusa, 1904. — *Naturalista sicil.* 17 : 109. Locus typicus : Sicily, Castelbuono. Type material : unknown. Unavailable name. Infrasubspecific taxon.

“*Satyrus semele blachieri* nov. subsp. nov.” Fruhstorfer, 1908. — *Ent. Z., Frankf. a. M.* 22 : 93. Locus typicus restrictus : Italy ; Sicily, Le Madonie (Kudrna, 1977 : 109). Type material : lectotype ♀, paralectotype ♀, in Muséum d’Histoire Naturelle, Genève ; design. Kudrna (1977 : 109). — Junior subjective synonym of *Eumenis (Satyrus) semele semthes* Fruhstorfer, 1908, **syn. n.**

“*Satyrus Semele*, Linné, race *Siciliana*, Obthr.” Oberthür, 1914. — *Études de Lépidoptérologie comparée* 10 : 130. Locus typicus : Sicily. Type material : lectotype ♀, paralectotype ♀, in The Natural History Museum, London ; **design. here Olivier & Coutsis.** — Junior subjective synonym of *Eumenis (Satyrus) semele semthes* Fruhstorfer, 1908, **syn. n.**

“*Satyrus semele* L. f. n. *neapolitana*” Stauder, 1921. — *Dt. ent. Z. Iris* 35 : 29. Locus typicus : “Höhenlagen im Neapolitanischen” [Monte Faito, cf. Stauder, 1923–1924a[1924] : 7 “loc. class. Faitogebiet”]. Type material : lectotype ♂, paralectotypes 1 ♂, 4 ♀, in The Natural History Museum, London, 2 ♂, in Narodni Prirodovedecka Museum (National Natural History Museum), Prague ; **design. here Olivier & Coutsis.** — Junior subjective synonym of *Eumenis (Satyrus) semele semthes* Fruhstorfer, 1908, **syn. n.**

“*Hipparchia semele* L. *blanchieri*” Troníček, 1949. — *Acta ent. Mus. natn. Pragae* 26 : 8. — Subsequent misspelling of the name *blachieri* Fruhstorfer, 1908.

“*Hipparchia aristaeus* Bon. *turcica* de Lattin i.l.” de Lattin, 1950. — *Rev. Fac. Sc. Univ. Istanbul* 15, ser.B : 311. Locus typicus :

- [Turkey] Bosphorus area (Baltalımanı, Maltepe); Uludağ. Type material: 1 syntype ♀, Uludağ, in Biogeographische Sammlung der Universität des Saarlandes, Saarbrücken. — Junior subjective synonym of *Eumenis (Satyrus) semele senthes* Fruhstorfer, 1908 (Kudrna, 1977: 113; Hesselbarth, van Oorschot & Wagener, 1995: 900).
- “*Hipparchia algerica* Obth. *vallettai* n. ssp.” de Lattin, 1952. — *Entomologist's Rec. J. Var.* 64: 336. Locus typicus: Malta, Naxxar. Type material: holotype ♂, ex coll. Valletta, present depository unknown. — Junior subjective synonym of *Eumenis (Satyrus) semele senthes* Fruhstorfer, 1908, **syn. n.**
- “*Hipparchia semele* L. exerge *aristaeus* race *antherosenthes*” Verity, 1953. — *Entomologist* 86: 175. Locus typicus: [Greece] Macedonia, lower altitudes on Mount Olympus. — Unavailable name (Article 13(a) of ICZN). Nomen nudum (Kudrna, 1977: 117).
- “*Hipparchia (Hipparchia) semele* L. [eserge *aristaeus*] razza *senthes* sottorazza *antherosenthes* nov.” Verity, 1953. — Le Farfalle diurne d'Italia. Vol. 5. Divisione Papilionida. Sezione Nymphalina. Famiglia Satyridae: 305. Locus typicus: [Greece, Makedonía, Óros Ólimbos] Skála. Type material: unknown. — Junior subjective synonym of *Eumenis (Satyrus) semele senthes* Fruhstorfer, 1908. Infrasubspecific taxon (Kudrna, 1977: 117).
- “*Hipparchia (Hipparchia) semele* L. [eserge *aristaeus*] razza *senthes* sottorazza *antherosthenes*” Verity, 1953. — Le Farfalle diurne d'Italia. Vol. 5. Divisione Papilionida. Sezione Nymphalina. Famiglia Satyridae: 305. — Subsequent misspelling of the name *antherosenthes* Verity, 1953.
- “*Hipparchia aristaeus* Bonelli ssp. *valletti*” Varin, 1960. — *Bull. Soc. ent. Mulhouse* 1960: 17. — Subsequent misspelling of the name *vallettai* de Lattin, 1952 (see also Leestmans, 1965: 95, 1968: 303).
- “*Hipparchia algerica* Obth. *vallettai* n. ssp.” Valletta, 1972. — The Butterflies of the Maltese Islands: 37. — Junior objective synonym of *Hipparchia algerica* Obth. *vallettai* de Lattin, 1952 (Kudrna, 1977: 107, 109) and junior subjective synonym of *Eumenis (Satyrus) semele senthes* Fruhstorfer, 1908, **syn. n.**
- “*Hipparchia ballettoi* sp. n.” Kudrna, 1984. — *Fragm. ent.* 17: 238. Locus typicus: Italy: Napoli: Monte Faito. Type material: holotype ♂, in coll. Balletto, paratypes 6 ♂, 1 ♀, in colls. Balletto, Kudrna & Museo Civico di Storia naturale “Giacomo Doria”, Genova. — Junior subjective synonym of *Eumenis (Satyrus) semele senthes* Fruhstorfer, 1908, **syn. n.**

"*Hipparchia balletoi*" Munguira, 1995. — Conservation of butterfly habitats and diversity in European Mediterranean countries. *In* : Pullin, A. S. (Ed.) : Ecology and Conservation of Butterflies : 284, 354. — Subsequent misspelling of the name *ballettoi* Kudrna, 1984 (see also Dennis, 1997 : 62).

"*Hipparchia blachieri* (...) *vallettae* Jutzeler, Biermann, Hesselbarth, Russo, Sala & de Bros, 1997. — *Linn. belg.* 16 : 118. — Subsequent misspelling of the name *vallettai* de Lattin, 1952.

ILLUSTRATIONS. Plate 1, figs. 1–8 (various type specimens). Plate 2, figs. 1–5 & 7–8 (including various type specimens). Plate 4, figs. 7–8. Plates 11–16, each figs. 1–4 (androconial scales). Text figs. 19–23 (male genitalia). Text figs. 24–28 (female genitalia). Text fig. 29 (genitalia of lectotype ♂ of *Eumenis* (*Satyrus*) *semele senthes* Fruhstorfer, 1908). Text fig. 30 (genitalia of lectotype ♂ of *Satyrus semele* L. f. *neapolitana* Stauder, 1921).

MATERIAL EXAMINED (type-specimens not included). Turkey, Sivas : 1 ♂ in coll. ZMA ; Turkey, Adiyaman : 2 ♀ in coll. ZMA ; Turkey, Niğde : 3 ♀ in coll. ZMA ; Turkey, Adana : 2 ♂, 3 ♀ in colls. VLCA, ZMA ; Turkey, Içel : 3 ♂, 1 ♀ in colls. VLCA, ZMA ; Turkey, Konya : 15 ♂, 12 ♀ in colls. VLCA, ZMA ; Turkey, Afyon : 2 ♂, 5 ♀ in colls. VLCA, ZMA ; Turkey, Isparta : 1 ♂, 1 ♀ in coll. ZMA ; Turkey, Antalya : 58 ♂, 117 ♀ in colls. VLCA, ZMA ; Turkey, Denizli : 1 ♀ in coll. ZMA ; Turkey, Muğla : 3 ♂, 3 ♀ in colls. VLCA, ZMA ; Turkey, İzmir : 2 ♀, in coll. VLCA ; Turkey, Ankara : 1 ♂, 1 ♀ in colls. ZMA, JGC ; Turkey, İstanbul : 9 ♂, 16 ♀ in coll. ZMA ; Bulgaria : 3 ♂, 4 ♀ in coll. VLCA ; Greece, Eastern Aegean islands, Kós : 4 ♂, 2 ♀ in coll. VLCA ; Greece, Eastern Aegean islands, Léros : 1 ♂ in coll. VLCA ; Greece, Eastern Aegean islands, Sámos : 23 ♂, 8 ♀ in coll. VLCA ; Greece, Eastern Aegean islands, Ikaría : 16 ♂, 25 ♀ in coll. VLCA ; Greece, Eastern Aegean islands, Híos : 45 ♂, 38 ♀ in colls. VLCA, ZMA, JGC, NG ; Greece, Eastern Aegean islands, Lésvos : 10 ♂, 9 ♀ in colls. VLCA, NG ; Greece, Northern Aegean islands, Thássos : 1 ♂ in coll. JGC ; Greece, Northern Aegean Islands, Samothráki : 1 ♂ in coll. VLCA ; Greece, Kikládés, Santoríni : 4 ♂, 4 ♀ in colls. VLCA, JGC ; Greece, Kikládés, Mílos : 7 ♂, 6 ♀ in coll. JGC ; Greece, Kikládés, Sífnos : 3 ♂, 5 ♀ in coll. JGC ; Greece, Kikládés, Páros : 20 ♂, 12 ♀ in colls. VLCA, JGC ; Greece, Kikládés, Síros : 6 ♂, 2 ♀ in coll. JGC ; Greece, Kikládés, Ándros : 6 ♂, 13 ♀ in colls. VLCA, JGC ; Greece, Évia : 1 ♂ in coll. JGC ; Greece, Égina : 2 ♂, 1 ♀ in coll. JGC ; Greece, Ídra : 9 ♂, 3 ♀ in coll. JGC ; Greece, Spétses : 3 ♂, 1 ♀ in coll. JGC ; Greece, Thráki : 4 ♂, 4 ♀ in colls. VLCA, JGC,

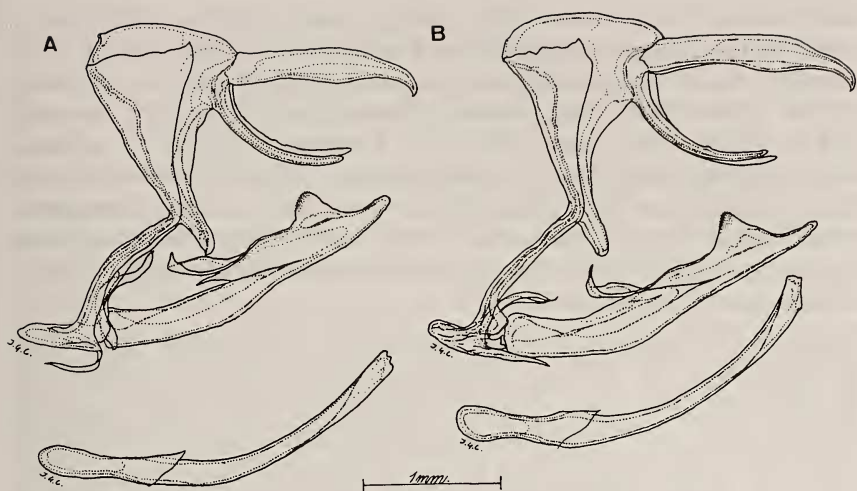


Fig. 19. *Hipparchia senthes* (Fruhstorfer, 1908) : male genitalia.

A. Turkey, Prov. Konya, Sultandağları, Akşehir (1100 m), 13/20.VII.1981, leg. H. & Th. van Oorschot & H. van den Brink, in coll. VLCA (Prep. JGC no. 2408). B. Greece, Eastern Aegean islands, Icaria, 1 km E. Monokámbi (450 m), 7.VI.1990, leg. A. Olivier, in coll. VLCA (Prep. JGC no. 2511).

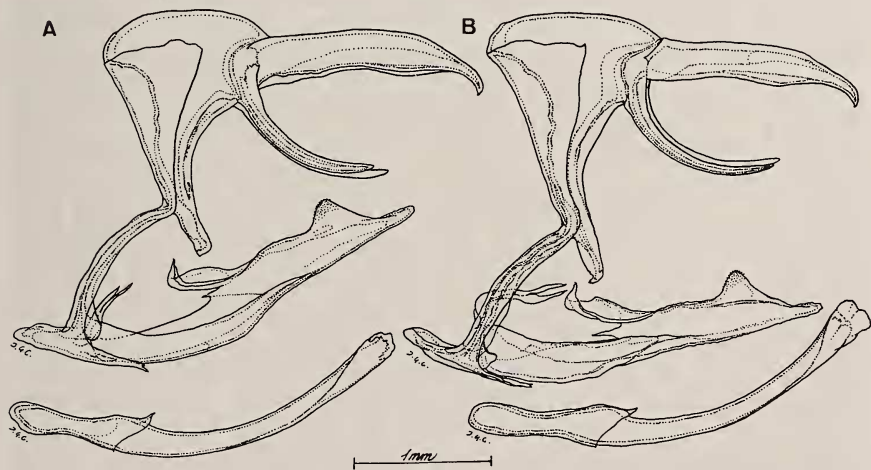


Fig. 20. *Hipparchia senthes* (Fruhstorfer, 1908) : male genitalia.

A. Greece, Pelopónissos, Lakonia, Óros Taígetos (1600 m), 15.VII.1983, leg. D. van der Poorten, in coll. VLCA (Prep. JGC no. 2503). B. Greece, Stereá Eláda, Fókida, Delfi (550 m), 20.V.1985, leg. A. Olivier, in coll. VLCA (Prep. JGC no. 2507).

NG ; Greece, Makedonía : 38 ♂, 20 ♀ in colls. VLCA, JGC, NG ; Greece, Stereá Eláda (mainly Óros Parnassós and Delfí) : 16 ♂, 15 ♀ in colls. VLCA, ZMA, JGC, NG ; Greece, Atikí : 16 ♂, 10 ♀ in colls. VLCA, ZMA, JGC, NG ; Greece, Pelopónissos : 11 ♂, 4 ♀ in colls. VLCA, ZMA, JGC ; Italy, Sicily, Le Madonie : 86 ♂, 79 ♀ in colls. VLCA, ZMA ; Italy, Calabria, Aspromonte : 2 ♂, 3 ♀ in coll. VLCA ; Italy, Calabria, La Sila : 19 ♂, 55 ♀ in coll. VLCA ; Italy, Campania, Ísola d'Íschia : 91 ♂, 7 ♀ in colls. VLCA, ZMA ; Italy, Campania, Ísola di Capri : 1 ♂ in coll. VLCA ; Italy, Campania, Monte Faito : 131 ♂, 25 ♀ in colls. VLCA, ZMA.

DESCRIPTION. Forewing length : see table 1 ; on average larger than *H. maderensis*, *H. aristaeus* and males of *H. algerica*, overlap with the latter taxon in females from Antalya and Híos. Male upperside ground-colour as in *H. algerica* and *H. aristaeus*, blackish brown spots in s2 and s5 on forewing and in s2 on hindwing always present and most often with a white pupil, those on forewing well developed but not as large as in *H. algerica* ; markings subject to considerable individual and geographic variation in their expression : on forewing much reduced in specimens from Turkey, the Aegean islands and the Balkans, that have small or even vestigial creamy yellow patches distad (and sometimes proximad) of s2 and s5 and occasionally traces of the same colouring in s3 or s1b (completely unmarked specimens, except for the spots, are, however, extremely rare), material from Calabria (especially La Sila) is very similar, but in several specimens the markings are more complete and their colour is more orange, in Campania (Monte Faito, Íschia) the markings are even more complete and orange, as much developed as in *H. algerica* in the most extreme specimens, on Sicily most specimens have a more or less continuous row of orange patches, sometimes even more expressed than in *H. algerica* (there are, however, specimens with very much reduced markings everywhere, even on Sicily) ; sex brand sometimes as reduced as in *H. algerica* in part of the specimens from Turkey, the Aegean islands and the Balkans, but generally more extended than in the latter taxon, well into s1b and often touching v1, though not invading s1a in some Greek and nearly all Italian specimens, including the Sicilian ones ; hindwing with complete series of light orange-ochreous patches in s2-s5(6), that remain separated by broad brown underlining of the veins, in material from Turkey, the Aegean islands and the Balkans as well as in most specimens from Calabria, small and not extending much basad, much as in *H. algerica* (very rarely vestigial or even entirely absent in single specimens from Turkey and Sámos), becoming progressively larger and extending more basad in material from Monte Faito, Íschia and Sicily,

sometimes extending basad almost until the cell, as in *H. aristaeus* (and in *H. leighebi*), but even in the latter three areas casual specimens exist that are hardly distinguishable from Anatolian-Balkan material. Female with markings much more complete, facultatively with a shading of the same colour in the discal area in s1b-s3, sometimes even invading the cell; the latter feature singly in specimens from mainland Greece (Delfi) and the Kikládés, but more frequently in Calabria, Campania (Monte Faito, Íschia) and, as a rule, on Sicily; in material from Turkey, the Aegean islands and the Balkans, as well as part of the specimens from La Sila, the orange-ochreous patches in s2-s5(6) on upperside hindwing reduced, generally better expressed in material from Monte Faito, Íschia and Sicily, following a similar line of variation as with the male. Underside forewing quite variable: basal-discal area corresponding to area of sex brand of upperside more orange in male, usually bordered by a discal line that can be well marked, but sometimes non-existent; in the female usually a strongly marked brown to blackish brown discal line, with an orange to coffee brown basal-discal area and a lighter orange to creamy yellow postdiscal area in material from Turkey, the Aegean islands, the Balkans, Calabria and part of the specimens from Campania (Monte Faito, Íschia) and Sicily: in the two last regions the distinction between the basal-discal and postdiscal area is less pronounced and the discal line occasionally becomes blurred, single extreme females from Sicily almost exactly like *H. aristaeus*. Underside hindwing discal line usually distinctly bending distally in s4-s5, evenly rounded or pointed: both conditions in the male, predominantly the latter condition in the female, though not always so; white postdiscal band always well expressed in the male, less so in the female, in which it is often invaded by greyish mottling, though only infrequently entirely obliterated. Male genitalia distinctly larger than in *H. maderensis*, *H. algirica* and *H. aristaeus*, both in overall size and in the length of uncus, gnathos and penis and height of tegumen; uncus always more robust than in these three taxa, length of tegumen and vinculum superior to that in the other three species, except for single largest specimens of those, valve always longer and broader than in *H. maderensis*, *H. algirica* and most *H. aristaeus*, but there is overlap between the largest specimens of last-mentioned and the smallest *H. senthes*, uncus > tegumen (mostly between 1.2 and 1.3), in other respects like the other three species of this group; in SW. Turkey (Antalya, Muğla) and on Sicily most specimens with a distinctly short gnathos, but similar specimens in this respect are sometimes encountered among material from Calabria and Greece; overall size of male genitalia very large in specimens studied from the

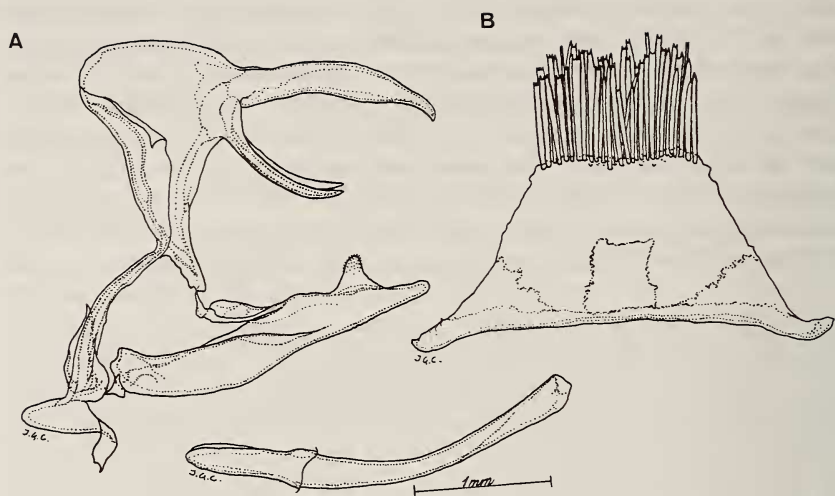


Fig. 21. *Hipparchia senthes* (Fruhstorfer, 1908) : male genitalia (A) and Jullien organ (B). Italy, Sicily, Prov. Palermo, Monti Le Madonie, Cozzo Pomieri, 7 km NW. Petralia Sottana (1150–1300 m), 17.VII.1991, leg. A. Olivier, in coll. VLCA (Prep. JGC no. 2278) (specimen illustrated on plate 2, fig. 5).

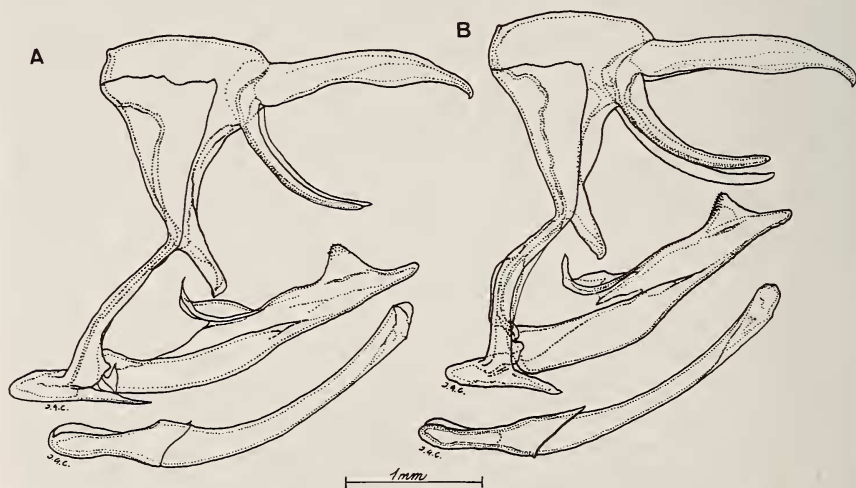


Fig. 22. *Hipparchia senthes* (Fruhstorfer, 1908) : male genitalia. A. Italy, Sicily, Prov. Palermo, Monti Le Madonie, Cozzo Pomieri, 7 km NW. Petralia Sottana (1150–1300 m), 17.VII.1991, leg. A. Olivier, in coll. VLCA (Prep. JGC no. 2277). B. Italy, Calabria, Prov. Cosenza, La Sila, Cerenzia (600–650 m), 27.VII.1995, leg. A. Olivier, in coll. VLCA (Prep. JGC no. 2358) (specimen illustrated on plate 2, fig. 3).

Kiklades (Síros, Mílos), distinctly smaller in material examined from SW. Turkey (Antalya, Muğla), that have the uncus and tegumen distinctly shorter than in any other material of *H. senthes*. Female genitalia sterigma usually larger than in other taxa of the *H. aristaeus* group and in superspecies *H. azorina*, but there is overlap, dorsal lamella as a rule larger than in other *H. aristaeus* group taxa, but with overlap, especially among material from Sicily, largest in material from the Pelopónissos and — especially — Calabria (La Sila), mid-dorsal process as in other *H. aristaeus* group taxa, but usually more pointed distally (in about one-fourth of the investigated specimens from Cerenzia (La Sila) slightly more elongated than in any other material of this group); corpus bursae usually larger than in the other three taxa of this group, especially on Sicily and in S. Italy, but there is some overlap, signum as a rule longer than in *H. maderensis*, *H. algerica* and *H. aristaeus*, but again there is overlap, though Sicilian material invariably has longer signa than any of these. Androconial scales not significantly variable geographically, but quite so individually, sometimes either short and broad or relatively long and slender in material from the same area; usually longer than in *H. (azorina) azorina*, *H. maderensis* and *H. algerica*, but rarely as long as in *H. (azorina) miguelensis* and *H. aristaeus* (plates 11 to 16, see also Kudrna, 1984 : 230, fig. 3).

DISTRIBUTION. *Turkey* : distributed over the western half of the country, including the European part, west of a line Tokat-Sivas-Malatya (see Hesselbarth, van Oorschot & Wagener, 1995 for a distribution map and a detailed locality list; additional data in Baraniak, Bakowski & Nowacki, 1994; Koçak, 1994; Koçak & Seven, 1994; Seven, 1995, 1996; Seven & Bakowski, 1996). *Bulgaria* : isolated colonies along the Black Sea coast (Arkutino) and near Sliven, more widespread in the S. and especially the SW. of the country (Struma valley, Ograzden Mt.) and in the Alibotush Mts. (Ganev, 1983, 1984, 1986, 1988; Abadjiev, 1993, 1995). *Former Yugoslav Republic of Macedonia* (e. g. in the Vardar valley : Titov Veles, Delčevo; see Jakšić, 1988 and Schaidler & Jakšić, 1989 for a distribution map). *Albania* (Kudrna, 1977; Abadjiev & Beshkov, 1996; Tolman & Lewington, 1997). *Greece*. As, until quite recently (Pamperis, 1997), no detailed distribution maps had been published for the butterflies of this country, we present an exhaustive list of localities, per province and nomos, for the mainland; for the islands, we generally do not enter into details about localities. Pamperis (1997) bases his identifications of the Greek *Parahipparchia* species on some characters of the pattern of male underside hindwing, that are unreliable, as the diagnostic features listed by him as species-

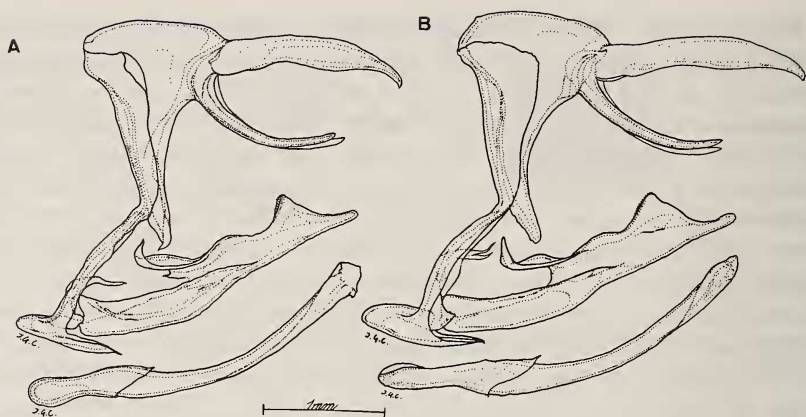


Fig. 23. *Hipparchia senthes* (Fruhstorfer, 1908) : male genitalia.

A. Italy, Campania, Prov. Nápoli, Monte Faito (1000-1100 m), 23.VII.1991, leg. A. Olivier, in coll. VLCA (Prep. JGC no. 2293). B. same data as A (Prep. JGC no. 2323).

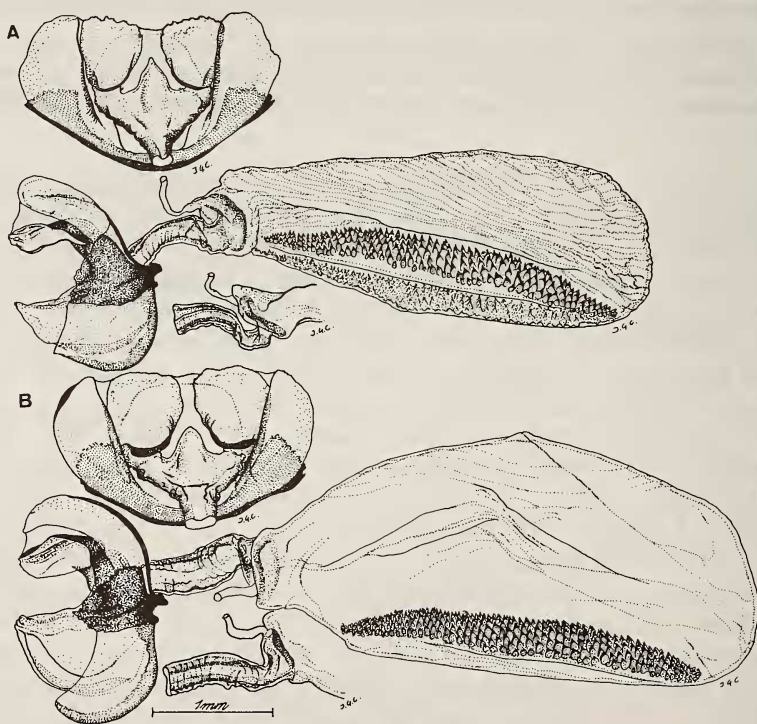


Fig. 24. *Hipparchia senthes* (Fruhstorfer, 1908) : female genitalia.

A. Greece, Eastern Aegean islands, Ikaría, Monokámbi (450 m), 6.VI.1990, leg. A. Olivier, in coll. VLCA (Prep. JGC no. 2518). B. Greece, Pelopónissos, Lakonía, Óros Taígetos (1600 m), 15.VII.1983, leg. D. van der Poorten, in coll. VLCA (Prep. JGC no. 2512).

specific for “*aristaeus*” [read *senthes*], for instance, do also occur in other species. Hence his distribution map should not be relied on, especially as far as records from western Makedonía and Ípiros are concerned. The following locality list is based on both personal data and reliable literature records. *GR, mainland*: Thráki — Évros (Didimótiho, Dadiá, Pessáni, Essími, Alexandroupoli), Xánthi (Óros Ahladóvouno, Xánthi); Makedonía — Dráma (Rodópi-Kará Deré, Paranésti, Livaderó, Óros Falakró, Káto Nevrokópi, Vólakas, Granítis, Pírgi, Katáfito, Mikrópolis), Séres (Óros Órvilos, Promahónas, Laíliás, Óros Vrondoús, Óros Meníkio, Séres, Óros Kerkíni), Kilkís (Kendrikó, Kilkís), Péla (Lake Vegoritída, Óros Kaïmaktsalán), Péla-Flórina (old road from Édessa to Flórina), Flórina (Óros Varnoúndas, Vronderó), Imathía (Náoussa, Óros Vérmio), Pieriá (Óros Ólimbos: Litóhoros, Ágios Dioníssios, Skála, Leptokariá); Thessalía — Lárissa (Óros Ólimbos-Kariá, Vólos), Tríkala (Metéora, cf. Hecq, 1991: possibly *H. volgensis*, confirmation required); Ípiros — Préveza (Párga, cf. Essayan & Cintré, 1980: possibly *H. volgensis*, confirmation required); Stereá Eláda — Etolía-Arkananía (Amfilohía), Fthiótida (Pournaráki Pass, Óros Parnassós), Fókida (Delfí), Viotía (Aráhova), Atiki-Piréas (Inói, Óros Párnis, Néa Makrí, Óros Pendéli, Ekáli, Dáfni, Athína, Athína-Ellinikó, Voúla, Haidári, Óros Imitós, Cape Souínio); Pelopónissos — Argolída (Tírintha, Óros Artemíssio), Korinthía (Óros Kilíni), Ahaía (Óros Helmós, cf. Brown, 1977, p. 155: “It is extremely rare on Mt. Chelmos (Vytina) and flies in pine forests at about 1200 m in June” [sic!]; we have been unable to trace this locality, but there is a place called Vitína in the nómos Arkadía), Arkadía (Óros Ménalo, Trípoli, Mantiréa, Ágia Sofía, Voúrvoura), Lakonía (Monemvassía, Areópoli, Óros Taígetos), Messinía (Langáda). *GR, islands*: Ionian islands — Lefkáda (Tsoukaládes, Nidrí, cf. Willemse, 1981: possibly *H. volgensis*, confirmation required); Spétses; Ídra; Égina; Évia (Psakhná, Oxílihos); Kikládés — Ándros, Síros, Náxos, Páros, Sífnos, Mílos, Folégandros, Kardiótissa, Santoríni; Vories Sporádes — Skíros; Northern Aegean islands — Thássos, Samothráki; Eastern Aegean islands — Lésvos, Híos, Sámos, Ikaría, Léros, Kós (sources: Staudinger, 1870; Fletcher, 1901; Fontaine, 1902; Rebel, 1902–1905, 1935, 1936, 1937, 1939a; Fruhstorfer, 1908a; Querci, 1935; Verity, 1936–1937, 1938–1939, 1953a, 1953b; Hartig, 1940; Reisser, 1946; Bernardi, 1961, 1971; Johnson, 1965; Bretherton, 1970; Higgins & Riley, 1970; Koutsaftikis, 1970, 1974a, 1974b, 1974c; de Worms, 1972, 1979; Coutsis, 1972, 1984, 1985a, 1985b, 1992, 1994, 1996; Cribb, 1974; Bigger, 1974; Brown, 1977; Kudrna, 1977; Dacie, Dacie & Grammaticos, 1977; Asselbergs, 1978; Dacie *et al.*, 1979; Essayan & Cintré,

1980 ; Löser, 1980 ; Willemse, 1981 ; Wiemers, 1983 ; Ulrich, 1985 ; Gaskin & Littler, 1986, 1988 ; Olivier, 1986, 1987, 1993, 1996, 1997 ; Olivier & De Prins, 1989 ; Luckens, 1990 ; Littler, 1991 ; Hecq, 1991 ; Cuvelier & Spruytte, 1994 ; Wakeham-Dawson, 1995, 1996 ; Holloway, 1996 ; Olivier & R. De Prins, 1996 ; Coutsis, De Prins, Dils, Ghavalas, Olivier & van der Poorten, unpublished records). Erroneously reported from Kríti (Mathew, 1898 ; Fletcher, 1901 ; De Prins & Iversen, 1996) and Ródos (Hesselbarth, van Oorschot & Wagener, 1995) : on the former island only *H. cretica* is known to exist, while no *Parahipparchia* taxon at all is known from the latter island (Olivier, 1993). *Italy* : Sicily — widely distributed in the northern and eastern part of the island : Monte Madonie, Monte Nebrodi, Monte Iblei, Etna, Monte Peloritani (Sichel, 1963 ; Kudrna, 1977 ; Leigheb, 1978 ; Cernigliaro, Di Benedetto & Lombardo, 1994 ; Tolman & Lewington, 1997) ; Calabria — Aspromonte, La Sila (Cesaroni *et al.*, 1994 ; Olivier, pers. obs. July 1995) ; Campania : Monte Faito, Íschia, Capri (Stauder, 1914–1915, 1917, 1921, 1923–1924a, 1923–1924b ; Kudrna, 1984 ; Kudrna & Leigheb, 1988 ; Jutzeler *et al.*, 1997 ; this study). *Malta* : reported at least once, but the butterfly certainly is not a resident there (de Lattin, 1952 ; Valletta, 1972 ; Sammut, 1984).

BIONOMICS. *Turkey, the Aegean islands and the Balkans.* Haploid chromosome number : $n = 29$ (Turkey, Amasya, cf. de Lesse, 1960 : 32). In Turkey, this species lives in a variety of flower-rich, poor grassland habitats at the edge of pine, cedar and evergreen oak forests of the mediterranean zone as well as of oak, beech and pine forests of the euxinian and subeuxinian zone ; the butterfly is often still found in remnants of destroyed forests. In open steppe-like habitats one will search in vain for it. The butterflies rest on tree trunks, on rocks and on the ground or in rocky crevices along paths and roads. Especially in the morning they look for such places in order to increase their body temperature, and towards the evening as well they try to benefit from the last sunbeams (Hesselbarth, van Oorschot & Wagener, 1995). On the Eastern Aegean islands, one of us (AO) noted the species in a series of seral stages from degraded garrigue, over bushy maquis to pinewoods. As the season advances, it becomes more strictly associated with pine forests, often sitting on the trunks, when sometimes up to almost ten specimens can be chased off one single trunk (e. g. on Híos and Sámos ; pers. obs., 1986–1990). On Ikaría it seems to be restricted to *Arbutus unedo* L. and *Erica arborea* L. dominated maquis (pers. obs., 1988 & 1990). On Kós it has been found only on Óros Díkeos, flying near (and nectaring on) thistles in open windswept areas near the summit at ca. 800 m (pers. obs., 1988 &

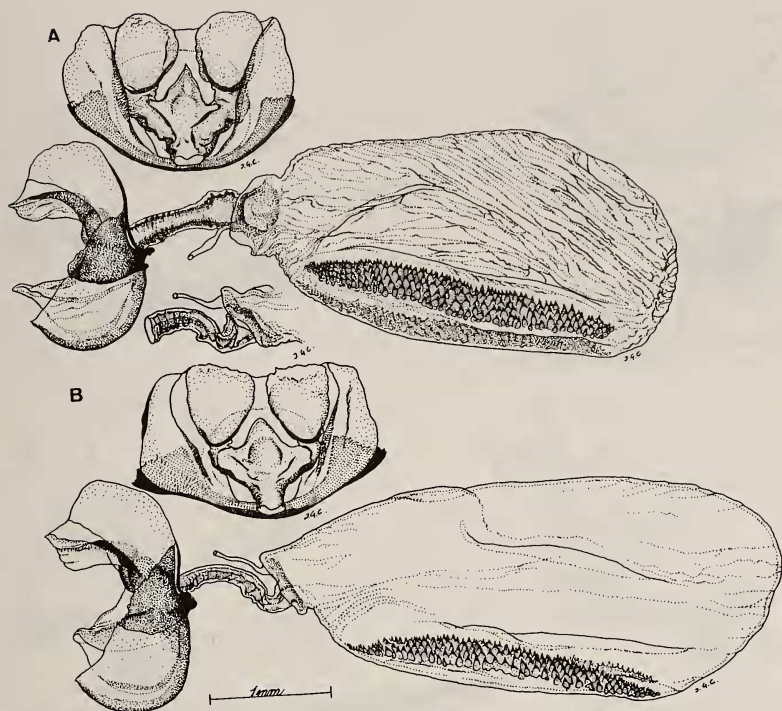


Fig. 25. *Hipparchia senthes* (Fruhstorfer, 1908) : female genitalia.
 A. Greece, Stereá Eláda, Fókida, Delfí (550 m), 20.V.1985, leg. A. Olivier, in coll. VLCA (Prep. JGC no. 2513). B. same data as A (Prep. JGC no. 2516).

1992). On Léros one single male was found in an orchard, flying off from under a *Ficus* tree (pers. obs., 1992). On the Kikládes, one of us (JGC) found it mostly associated with orchards and cultivated areas, on Ándros near the shaded trunks of plane trees and olive trees (Coutsis, 1985a), on Santoríni near *Ficus* trees (Coutsis, 1992). In mainland Greece we both encountered it in garrigue, maquis, cultivated areas, pine forest (*Pinus halepensis* Miller and *P. brutia* Ten.), fir forest (*Abies cephalonica* Loudon), mixed evergreen-deciduous forest and deciduous forest. In the north of Greece also in steppe-like areas (Coutsis, pers. obs.). In Bulgaria, Abadjiev (1993) reports it as “An inhabitant of arid rocky formations near mixed forests with predominance of xerothermic oaks in Kresna Gorge, Kozhuh Hill, etc. The butterfly flies along bushes, low trees, often resting on stones, tree trunks”. In Turkey, *H. senthes* has been observed from (almost) sea

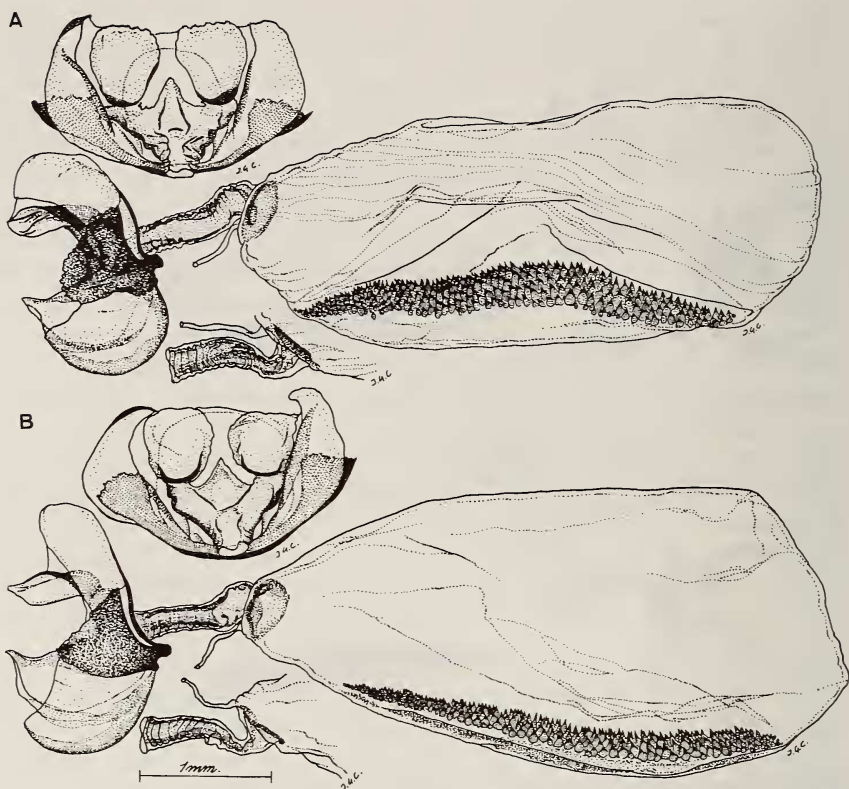


Fig. 26. *Hipparchia senthes* (Fruhstorfer, 1908) : female genitalia.

A. Italy, Sicily, Prov. Palermo, Monti Le Madonie, Cozzo Pomieri, 7 km NW. Petralia Sottana (1150–1300 m), 17.VII.1991, leg. A. Olivier, in coll. VLCA (Prep. JGC no. 2452). B. same data as A (Prep. JGC no. 2453).

level (Muğla, Bodrum Peninsula ; Olivier, pers. obs. 1988) up to 1900 m in Antalya, Palaz Dağı, 2000 m on the Uludağ (Bursa) and even 2100 m in Niğde, Aladağları (Hesselbarth, van Oorschot & Wagener, 1995). On the Aegean islands, the butterfly is known from sea level (Littler, 1991) up to 1297 m on Óros Pelinéo on Híos (Olivier, pers. obs. 1990). On the Greek mainland it has been found from sea level up to 1700 m (Coutsis, pers. obs.), while according to Pamperis (1997) it has been encountered as high as 1900 m. It has been observed taking nectar on *Thymus* sp. (Lamiaceae) (Koçak, 1990a), *Rubus* sp. (Rosaceae) and *Sambucus ebulus* L. (Caprifoliaceae) (Hesselbarth, van Oorschot & Wagener, 1995). Pamperis (1997) shows several specimens taking nectar

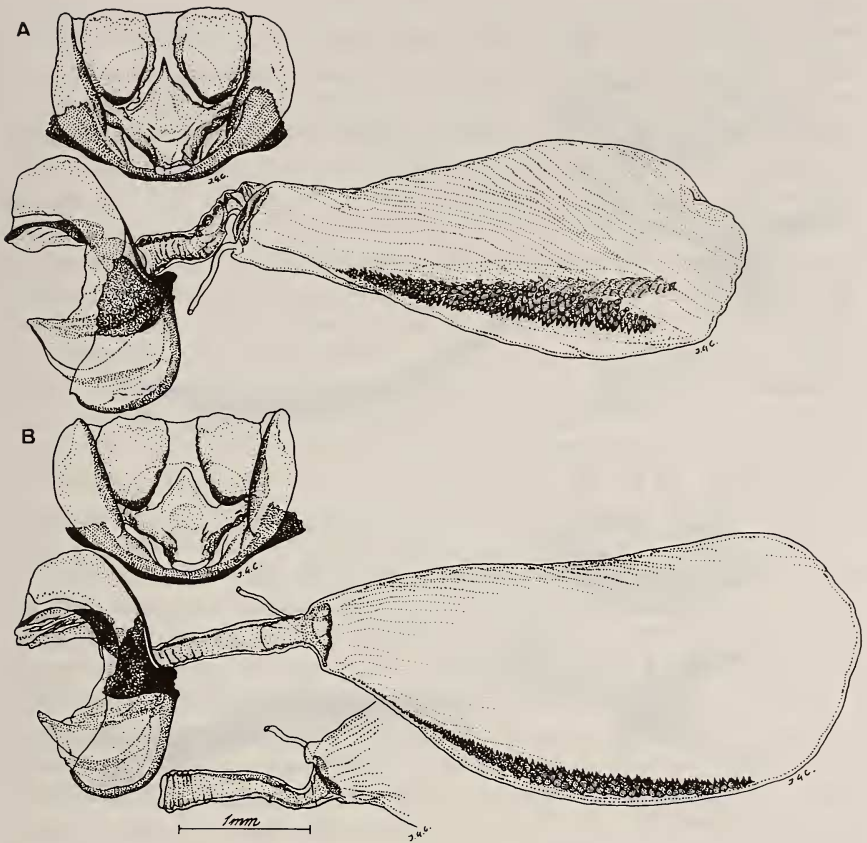


Fig. 27. *Hipparchia senthes* (Fruhstorfer, 1908) : female genitalia.
 A. Italy, Calabria, Prov. Cosenza, La Sila, Cerenzia (600–650 m), 27.VII.1995, leg. A. Olivier, in coll. VLCA (Prep. JGC no. 2380). B. Italy, Calabria, Prov. Cosenza, La Sila, Cerenzia (600–650 m), 28.VII.1995, leg. A. Olivier, in coll. VLCA (Prep. JGC no. 2382).

from various flowers. One of us (AO) observed it drinking from mud as well as from the fallen fruits under mulberry (*Morus alba* L.) trees (Moraceae) on Híos (Nagós, 50 m) in midsummer (21.VII.1988), a behaviour it shared with *Hipparchia syriaca* (Staudinger, 1871), *H. fatua* Freyer, [1777], *Maniola chia* Thomson, 1987 and *Kirinia roxelana* (Cramer, [1777]). Univoltine : the flight period starts in the third week of May at Delfí (central Greece), on Sámos and on Híos (Eastern Aegean islands) and on the Bodrum Peninsula (Turkey) (de Worms, 1972 ; Olivier, pers. obs. 1985–1988) ; on the islands of Folégandros

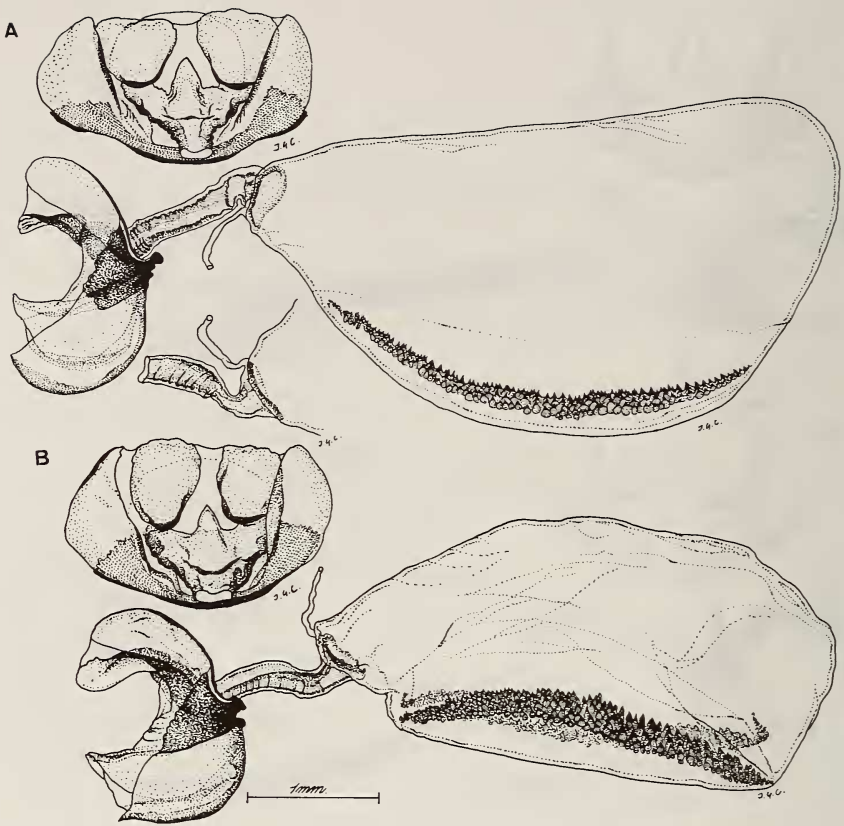


Fig. 28. *Hipparchia senthes* (Fruhstorfer, 1908) : female genitalia.

A. Italy, Campania, Prov. Nápoli, Monte Faito (1000–1100 m), 22.VII.1991, leg. A. Olivier, in coll. VLCA (Prep. JGC no. 2456). B. same data as A (Prep. JGC no. 2458).

and Kardiótissa (Kykládes) it has been found as early as 10/12.V. (Rebel, 1935) and on Síros even on 6/7.V.1995 (Coutsis, 1996). Remarkably, Fletcher (1901) encountered it on 27.IV at Tírintha near Náfplio (Pelopónissos, Argolída), but this is exceptional. It lasts throughout the summer with peaks in June–July in Greece and July–August in Turkey (Kudrna, 1977) until as late as the middle of October (Hesselbarth, van Oorschot & Wagener, 1995). According to Pamperis (1997), the flight period in Greece is from May to October. From Bulgaria, the flight period is stated by Ganev (1986) as “6–11” (!). Early stages, larval biology and larval host-plants unknown. The extended flight period suggests adult aestivation at least in the

mediterranean zone of Turkey and on the Eastern Aegean islands (Gaskin & Littler, 1988 ; Hesselbarth, van Oorschot & Wagener, 1995), as well as in mainland Greece (e. g. Óros Imitós (400 m), 16.IX.1988, 1 ♀ leg JGC) and in Bulgaria (Ganev, 1984, 1986). It is worth mentioning that Koçak (1989a) reports a migration of *H. senihes*, involving both sexes, on 9.VII.1988 at Kayalyatak, in the Ayas district in the province of Ankara (Turkey). Such behaviour was also noticed by one of us (JGC) in Greece. Feltwell (1976) discusses a migration of *H. semele* in southern France, while Hesselbarth, van Oorschot & Wagener (1995) also mention what is possibly a migration of *H. pellucida* near Uludere (Şırnak) in SE. Turkey. Such mass movements are, however, very rare events.

Sicily. The habitat consists of dry rocky ground with sparse bushes and trees (especially fig, carob and olive trees), orchards and occasionally open oak woodland, rarely pine or chestnut woods (though von Kalchberg, 1872 reports it “in grosser Menge, im Schatten des Kastanienlaubes Kühlung suchend”). It settles mostly on stones, rocks, bare ground and tree trunks, but — according to Leigheb (1978) — seldom on flowers (Bigger, 1977 ; Leigheb, 1978). One of us (AO) had the opportunity to observe this species in three localities of the Monte Madonie (Palermo) in July 1991. At Castelbuono (500 m) it was found commonly, sitting on tree trunks and branches in the shade, in a few apple tree orchards (15.VII) ; 3 km N. Petralia Sottana (900 m) it occurred frequently in oak woodland clearings, sitting on the ground as well as under small bushes (16.VII). Finally, at Cozzo Pomieri, 7 km NW. Petralia Sottana (1150–1300 m), it was often seen while taking nectar on a blue thistle species near the valley bottom and in adjoining grasslands uphill on open, rocky ground. Its numbers quickly dropped as one went higher up, and it was almost entirely absent on reaching wet acid meadows just below the line of beech forest. It is noteworthy that, in localities at lower altitudes, the butterfly is often closely associated with trees, being restricted to shady places (von Kalchberg, 1872 ; Bigger, 1977 ; Olivier, pers. obs. : vide supra). It is usually found at altitudes from 500 up to about 1500 m, sometimes as high as almost 1900 m, while its lower limit may descend to about 400 m and occasionally even to sea level (Sichel, 1963 ; Kudrna, 1977 ; Leigheb, 1978 ; Cernigliaro, Di Benedetto & Lombardo, 1994). One single protracted brood from the last third of May to September, sometimes even October, with one record as late as 5.XI (Ragusa, 1904 ; Sichel, 1963 ; Leigheb, 1978 ; Cernigliaro, Di Benedetto & Lombardo, 1994). Early stages, larval biology and larval host-plants unknown. The extended flight period is suggestive of adult aestivation.

S. Italy. In July 1995, one of us (AO) was able to observe this taxon both in Aspromonte (5–8 km SSE. Gambárie (1600–1700 m), 23 & 24.VII.1995) and in La Sila (Cerenzia (600–650 m), 26–28.VII.1995), thereby confirming a previous mention by Cesaroni *et al.* (1994). In the latter locality, 1 ♂, 1 ♀ had previously been collected on 2.VI.1975 and, in a nearby locality — San Giovanni in Fiore (1100 m) — 1 ♀ was found on 1.VI.1975 (Gallo & Cassulo, in litt.). The Aspromonte locality was a flower-rich roadside in a beech forest, while Cerenzia was a small, dense, pine wood, where the butterflies were congregating on the tree trunks, flying off only when disturbed. The male-female ratio was estimated at about 1:15. In Campania, the butterfly is known from the Monte Faito area on the Sorrento Peninsula (Nápoli), where it is met with on poor grasslands on limestone hills with many flowers, as well as in forest clearings in beech woodland, from as low as 130 m at Vico Equense up to the summit at 1100 m. Recorded nectar sources appear to change as the season advances, including *Spartium junceum* L. (Fabaceae), *Thymus* sp. (Lamiaceae), *Santolina* sp. (Asteraceae) and *Eryngium amethystinum* (Umbelliferae). After humid nights or rainfall it sits on the roads. Early in the season, males show strong territorial behaviour, pursuing every approaching butterfly, especially in the morning and again from about 4 p.m. until sunset. During the hottest hours of the day, activity is reduced to a minimum. Females also fly in the morning and disappear in the afternoon. As the season progresses, males become scarcer, disappearing completely by late August. Larval host-plants: various Poaceae. Jutzeler *et al.* (1997) mention *Festuca* spp. (*jeanpertii* or *circummediterranea*) and *Brachypodium distachyum* as predominating in its habitat on Monte Faito. Larvae in captivity accepted both these grass species, as well as *Festuca ovina* and *Poa annua*. The flight period starts in June and lasts until at least the end of August (Stauder, 1914–1915, 1923–1924a, 1923–1924b; Cesaroni *et al.*, 1994; Jutzeler *et al.*, 1997). One of us (AO) observed this butterfly in the higher parts of Monte Faito (1000–1100 m) on 22 & 23.VII.1991. While some specimens were seen in clearings along the road in the beech forest, it was found in good numbers only near the top, on bare calcareous soil and on adjoining flower-rich slopes near the summit. Butterflies were often nectaring on a blue thistle species. Early stages: described in detail by Jutzeler *et al.* (1997). According to these authors, females collected in June failed to lay any eggs and oviposition took place after a rather long period, strongly suggesting delayed ovarian maturation. The species has also been recorded on the island of Íschia, where it has been observed along the southern coast, north of San Angelo, as well as in some lowland

localities at 200–400 m (Ciglio, Fontana), penetrating vineyards (Kudrna & Leigheb, 1988 ; Jutzeler *et al.*, 1997 ; Olivier, pers. obs. 8 & 9.VII.1991). One of us (AO) found it to be extremely common on the western slopes of Monte Epomeo (600–780 m), the males still very fresh and the very first females just emerging. There males were sitting on the bare ground along a rocky path in poor dry grassland. Butterflies were also commonly taking nectar on blossoms of *Castanea sativa* Mill. It has been reported on this island from early June until August (Kudrna & Leigheb, 1988).



Fig. 29. Lectotype of *Eumenis (Satyrus) semele senthes* Fruhstorfer, 1908 [= *Hipparchia senthes* (Fruhstorfer, 1908)] : genitalia (specimen illustrated on plate 2, fig. 7).

SYMPATRY WITH RELATED TAXA. *Hipparchia senthes* is the only taxon treated in the present revision that is known to be sympatric with other *Parahipparchia* taxa, all belonging to the *Hipparchia semele* group (cf. section 1.3). In Turkey, it is syntopic and synchronous in several localities with either *H. mersina* or *H. pellucida* or both in Anatolia, with *H. volgensis* in the province of Kırklareli in the European part (Hesselbarth, van Oorschot & Wagener, 1995). On the Eastern Aegean islands it was found syntopic and — at least partly — synchronous with either *H. mersina* (Sámos), *H. pellucida* (Ikaria) or both (Lésvos) (Olivier & De Prins, 1989 ; Olivier, 1993). On the Greek mainland, one of us (JGC) encountered it syntopic and synchronous with *H. volgensis* in several localities in the western part of Makedonia (Óros Kaïmaksalán, along the old road from Édessa to Flórina, Óros Varnoúndas, Vronderó) and such is also the case on the Pelopónissos as far south as on Óros Taígetos (Ichtiaroglou, pers. comm., see also Ulrich, 1997). Sympatry of *H. senthes* with *H. volgensis* certainly

occurs as well in Bulgaria (Abadjiev, 1993) and in the Former Yugoslav Republic of Macedonia (Schneider & Jakšić, 1989) and is most likely to exist also in Albania. As both taxa look absolutely identical externally (the wing characters listed by Pamperis, 1997 as species-specific are not, being too variable and with a substantial degree of overlap between species), old records of *Hipparchia semele* (or “*Satyrus semele*”) from the southern Balkans may apply to either *H. senthes* or *H. volgensis*. As a result, we have only considered distribution records that are absolutely reliable. We do not know of any substantiated record of sympatry of *H. senthes* with *H. semele* in the Balkans. On Sicily and in Calabria, *H. senthes* is syntopic and synchronous with *H. semele* in many localities (Sichel, 1963 ; Kudrna, 1977 ; Leigheb, 1978 ; Cernigliaro, Di Benedetto & Lombardo, 1994 ; Cesaroni *et al.*, 1994 ; Olivier, pers. obs. July 1991 & 1995), but in Campania (Monte Faito, Íschia, Capri) only *H. senthes* is known to occur.

COMMENTS. Before discussing the reasons that led us to the present conclusions, especially concerning the Sicilian and south Italian populations, it is useful to review the taxonomic views on the subject



Fig. 30. Lectotype of *Satyrus semele* L. f. *neapolitana* Stauder, 1921 [= *Hipparchia senthes* (Fruhstorfer, 1908)] : genitalia (specimen illustrated on plate 1, fig. 5).

up to the present. As prior to this study two, or even three species of the *H. aristaeus* group were believed to exist within the distribution area of *H. senthes*, we will discuss the situation separately for Turkey, the Aegean islands and the Balkans, Sicily, Malta and S. Italy. Old catalogues and standard works, covering the whole of Europe and Asia Minor, only mention "*Satyrus* [or *Hipparchia*] *semele*" for the whole area (Staudinger, 1871; Lang, 1884; Heyne, 1895; Tutt, 1896; Staudinger & Rebel, 1901; Kirby, 1903; Seitz, 1908; Spuler, 1908; Oberthür, 1909).

Turkey, the Aegean islands and the Balkans. Early authors simply listed it as "*Satyrus semele*" (Staudinger, 1870; Fontaine, 1902; Rebel, 1902–1905), with one notable exception (Fletcher, 1901, who lists it as "*Hipparchia semele* var. *aristaeus*"), until Fruhstorfer (1908a) described it as "*Eumenis (Satyrus) semele senthes*" from Óros Taígetos (Pelopónissos, southern Greece). It was subsequently treated under this subspecific combination (either as a "form", "race", "var.[iety]" or "ssp.") by most subsequent ones until 1949 (Rebel, 1910, 1916; Verity, 1923–1924, 1925, 1936–1937, 1938–1939; Graves, 1926; Gaede, 1931; Jachontov, 1935; Heydemann, 1942; Reisser, 1946), although several authors continued to list it simply as "*H. semele*" until very recently (Barraud, 1918; Buresch & Tuleschkov, 1929; Querci, 1935; Rebel, 1937, 1939a; Johnson, 1965; Koutsaftikis, 1970; Fuchs, 1992). Some have mentioned it erroneously as "*semele cadmus*" (Rebel, 1935; D'Abbrera, 1992), "*semele mersina*" (Verity, 1938–1939; Tuleschkov, 1951) or even "*semele cretica*" (Rebel, 1936; Hartig, 1940). In his revision of the "*Hipparchia semele* Gruppe", de Lattin (1949) treated *senthes* as a subspecies of *Hipparchia aristaeus*, in which he was followed by Varin (1960), Leestmans (1965, 1968), Bretherton (1966), Higgins & Riley (1970, 1984), de Worms & Bretherton (1975), Weiss (1975), Zangheri (1975), de Worms (1979), Dacie *et al.* (1979), Holloway (1979, 1996), Essayan & Cintré (1980), Baldock & Bretherton (1981), Higgins & Hargreaves (1983), Coutsis (1984), Gaskin & Littler (1986, 1988), Leestmans & Arheilger (1987–1988), Olivier & De Prins (1989), Gaskin (1990), Luckens (1990), Verhulst (1990), Littler (1991), D'Abbrera (1992), Spruytte (1992), D'Hondt *et al.* (1992), Olivier (1993), Cuvelier & Spruytte (1994), Kolev (1994), Hesselbarth, van Oorschot & Wagener (1995), Wakeham-Dawson (1995, 1996), De Prins & Iversen (1996), Ulrich (1997) and Tolman & Lewington (1997), although several authors continued to report it as a subspecies of *H. semele* (Daniel, Forster & Osthelder, 1951; Thurner, 1964, 1967; Eckweiler, 1977; Schurian & Hofmann, 1983). Both a broader species concept and nomenclatural confusion (vide supra, comments under both *H. algirica*

and *H. aristaeus*) have led to it being listed as well as *H. aristaeus* (de Lesse, 1960; Bernardi, 1961; Sichel, 1962; Stempffer, 1962; Higgins, 1966; Bretherton, 1968, 1970; Coutsis, 1969, 1972, 1985a, 1985b, 1992, 1994; Robinson, 1971, 1990; de Worms, 1972; Koutsafikis, 1974a, 1974b, 1974c; Bigger, 1974; Cribb, 1974; Schaidler & Jakšić, 1989; Gaskin & Littler, 1993; Withrington, 1995; Pamperis, 1997), *H. algerica* (Schmidt-Koehl, 1969; Kudrna, 1975; Asselbergs, 1978; Koçak, 1981–1983, 1989a, 1989b, 1989c, 1990a, 1990b, 1994; Ulrich, 1985; Jakšić, 1988; Schaidler & Jakšić, 1989; Koçak & Seven, 1991, 1994; van Oorschot & van den Brink, 1991, 1992; Baraniak, Bakowski & Nowacki, 1994; Seven, 1994, 1995; Seven & Bakowski, 1996), *H. algerica senthes* (Kudrna, 1977; Brown, 1977; Dacie, Dacie & Grammaticos, 1977; Milošević & Lorković, 1978; Goossens & Cromphout, 1978; Goossens, 1979; Hofmann, 1979; Löser, 1980; Schmidt-Koehl, 1980; Willemse, 1981; Wiemers, 1983; Jakšić, 1983; Ganev, 1983, 1984, 1985a, 1985b, 1986; Fuchs, 1985; Taymans & Taymans, 1985; Schmidt & Hassler, 1986; Kiriakov, 1988; Schmidt, 1989; D'Hondt *et al.*, 1992; Seven, 1996; Koçak, 1996) or even *H. aristaeus algerica* (Higgins, 1975; Vassilaina-Alexopoulou & Mourikis, 1985). Kudrna (1984, 1986, 1996) elevated *senthes* to full species rank, in which he has since been followed by Taymans & Taymans (1985), Olivier (1986, 1987, 1996, 1997), Ganev (1988), Gaskin & Littler (1989), Schaidler & Jakšić (1989), Taymans (1989), Balletto *et al.* (1990), Hecq (1991), Abadjiev (1993, 1995), Balletto (1995), Abadjiev & Beshkov (1996), Coutsis (1996), Olivier & R. De Prins (1996), Kolev & van der Poorten (1997), Dennis (1997) and Jutzeler *et al.* (1997): we treat it as such in the present study as well. It is quite funny to notice that a few authors have used two (Taymans & Taymans, 1985; D'Abbrera, 1992; D'Hondt *et al.*, 1992) or even three (Schaidler & Jakšić, 1989) different taxonomic combinations to designate this species within the same publication! From NW. Turkey, de Lattin (1950) described "*Hipparchia aristaeus* Bon. *turcica* de Lattin i.l.", while Verity (1953a, 1953b) described *antherosenthes* from Skála, on the lower slopes of Óros Ólimbos, as a (sub-)race of "*H. semele* L. *exerge aristaeus*": both taxa were synonymized by Kudrna (1977). Schmidt-Koehl (1969) reported a "ssp. nova" of "*Hipparchia algerica* Oberthür" from Amasya and Ankara in Turkey, but it has remained undescribed, a fact we can only welcome! As both *H. senthes* and *H. volgensis* occur on Óros Taígetos, it is fortunate that a lectotype has been designated for *H. senthes* and that its identity has been established unambiguously by Kudrna (1977: 116–117; compare text fig. 29 of present study). *Sicily*. The first record of which we know is that of "*S. arethusa* var. *aristaeus*" (!) by Costa (1840). Very soon it was realized that two related

taxa occurred on Sicily, that were initially considered as “varietas” of the same species : von Kalchberg (1872) reported “*Satyrus Semele* var. *Aristaeus* Bon.” from Castelbuono, in the lower parts of Le Madonie (p. 315), while recording “*Satyrus semele* L. (...) darunter selten var. *Aristaeus* Bon.” from “Madonia-Gebirge” (p. 317). He was followed in this by Lang (1884) and Heyne (1895), while Staudinger & Rebel (1901), Oberthür (1909) and Barrett (1912) list it as “*Satyrus semele* var. *algerica*”. Among the early authors, Ragusa (1904), Spuler (1908) and Barrett (1911) simply quote it as “*Satyrus semele*”. Fruhstorfer (1908b) described “*Satyrus semele blachieri* nov. subspec.” after two females in coll. Blachier [now in Muséum d’Histoire Naturelle, Genève]. These were designated as lectotype and paralectotype by Kudrna (1977) : they clearly do not belong to *H. semele*, as was erroneously stated by several authors (see below). Oberthür (1914) described “*Satyrus Semele*, Linné, race *Siciliana*, Obthr.” after two females collected by Bellier de la Chavignerie [now in The Natural History Museum, London] and that we designate here as lectotype and paralectotype : Ragusa (1916–1919) — and Kudrna (1977) after him — correctly pointed out that the name *siciliana* is a junior synonym of the name *blachieri*. The name *blachieri* was correctly ascribed to what we now consider to be *H. senthes* by Verity (1915, 1916), Rebel (1916), Ragusa (1916–1919), Stauder (1920–1923) and Mariani (1939). It is not clear what Stauder (1915–1916[1916]) exactly understands when mentioning *Satyrus semele blachieri*. Verity (1923–1924[1924]) made a mistake in distinguishing both Sicilian taxa under the respective names of *siciliana* for what we at present consider as *H. senthes* (this is correct!) and of *blachieri* for what we at present consider as *H. semele* (sic!), without having studied Fruhstorfer’s type specimens, stating explicitly on p. 25 : “In 1914, I made the mistake of describing in the *Bull. Soc. Ent. Italiana*, XLV., p. 219, the male of *siciliana*, Obth., as that of *blachieri*, but, now I am acquainted with the two Sicilian races, I can see that the darker one is that named by Frühstorfer”. This misinterpretation of the name *blachieri* was perpetuated by Verity (1925, 1953b), Gaede (1930, 1931), Schwingenschuss (1942), de Lattin (1949), Bernardi (1961) and Valletta (1976, 1978). As a result, Sicilian *H. senthes* was reported as “*Satyrus semele* L. *siciliana* Oberth.” by Gaede (1930, 1931), Verity (1938–1939[1938]) and Schwingenschuss (1942). In his revision of the “*Hipparchia semele* Gruppe”, de Lattin (1949) treated *senthes* from Sicily under the name “*Hipparchia aristaeus* Bon. Rasse *siciliana* Obth.”, in which he was followed by Varin (1960), Bernardi (1961), Bretherton (1965), Leestmans (1965, 1968), Higgins & Riley (1970, who treated it as “*H. aristaeus aristaeus* f. *siciliana*”) and Higgins (1975). Kudrna (1977) erroneously considered

blachieri as a subspecies of *H. algerica*, but correctly re-established it as the oldest available name for the “*aristaeus* group taxon” from Sicily, as understood at that time. The remainder of the story is analogous to what happened with *H. algerica*, *H. aristaeus* and *H. senthes* from Turkey and the Balkans, as a result of both a broader species concept and nomenclatural confusion: hence we find records as *H. aristaeus* (Sichel, 1962, 1963; Bretherton, 1966; Bigger, 1977; D’Abrera, 1992; Cernigliaro, Di Benedetto & Lombardo, 1994), *H. algerica* (Kudrna, 1975), *H. aristaeus blachieri* (Higgins & Hargreaves, 1983; Higgins & Riley, 1984; Coutsis, 1984; De Prins & Iversen, 1996; Tolman & Lewington, 1997), *H. algerica blachieri* (Kudrna, 1977; Leigh, 1978), *H. algerica siciliana* (de Lattin, 1952) and *H. blachieri* (Kudrna, 1984, 1986, 1996; Balletto & Kudrna, 1985; Taymans, 1989; Balletto *et al.*, 1990; Meyer, 1993; Balletto, 1995; Balletto & Cassulo, 1995; Jutzeler *et al.*, 1997; Dennis, 1997). As we consider the Sicilian population to be conspecific with those from the Balkans, the Aegean islands and Turkey, *senthes* becomes the oldest available name with both *blachieri* and *siciliana* as junior subjective synonyms (Fruhstorfer’s description of *senthes* was published on 11.IV.1908, that of *blachieri* on 5.IX.1908).

Malta. *H. senthes* is not a resident species on Malta: it has perhaps been observed twice there, and the first record is not certain. Sammut (1984) states (p. 85): “One example seems to have been taken by H. Harford at St. Julians on the 10th. September 1910”; this specimen could be either *H. senthes*, *H. algerica* or *H. semele*. A second specimen, a male collected by Valletta at Naxxar on 23.V.1939, served as a basis for the description by de Lattin (1952) of “*Hipparchia algerica* Obth. *vallettai* n. ssp.”. We haven’t seen this specimen, but there is an illustration of it in Valletta (1972) and Kudrna (1977), who examined the holotype, considered it “a worn specimen of *blachieri*”, consequently synonymizing *vallettai* under “*Hipparchia algerica blachieri*”. Previously, Verity (1953b) considered it as a “razza” (race) of “*Hipparchia (Hipparchia) semele* L. *eserge aristaeus* Bon.”. Subsequently, it was listed as a subspecies of *H. aristaeus* by Varin (1960), Bernardi (1961) and Leestmans (1965, 1968), while Bretherton (1966) simply quoted it as “*H. aristaeus*”. Valletta (1972) unintentionally redescribed it as “*Hipparchia algerica* Obth. *vallettai* n. ssp.”, thus creating at the same time a junior objective synonym and a junior homonym of de Lattin’s name. Cilia (1979) used the combination *H. algerica vallettai* again, and finally Sammut (1984) treated it as an infrasubspecific form of “*Hipparchia aristaeus algerica*”. As a result of our treatment of the names *blachieri* and *siciliana* (vide supra), *vallettai* automatically becomes a junior subjective synonym of *senthes*.

S. Italy. Before the First World War, authors listed this taxon respectively as “*Satyrus Semele* v. *Algirica* Obth.” (Staudinger & Rebel, 1901), “*Satyrus semele*” (Oberthür, 1909, p. 269 : “*Semele* du pays de Naples serait une forme agrandie du *Semele* français”; Stauder, 1914–1915[1915]), *Satyrus semele blachieri* Verity [sic!] (Stauder, 1915–1916 [1916], p. 60 : “*S.s.* Uebergang von *cadmus* Fruhst. zur nächstfolgenden Rasse *blachieri* Verity in ganz Unteritalien”) and “*Satyrus semele* trans. ad subsp. *blachieri* Obth.” (Stauder, 1917). Subsequently, Stauder (1921) describes “*Satyrus semele* L. f.n. *neapolitana*” (on p. 29) as “eine Uebergangsform zu *aristaeus* mit aufgehelltem Ockerbraun ; diese aus Höhenlagen im Neapolitanischen”, later specifying its type locality as Monte Faito (Stauder, 1923–1924a[1924], p. 7 : “Ich schlage daher für die Form aus Umgebung Neapel (loc. class. Faitogebiet, Ende VI, VII) den Namen *neapolitana*”). Some, mostly very recent, authors rightly consider this name as nomenclaturally available, either as a subspecies of *H. semele* (Varin, 1960) or as a distinct species (Jutzeler & de Bros, 1997 ; Jutzeler *et al.*, 1997 ; see also Cesaroni *et al.*, 1994). Indeed, while Stauder (1921) published some new names in the same publication as “subsp. n.”, and the next year (Stauder, 1920–1923[1922]) reported it again as “*Satyrus semele blachieri* Obth.”, thus clearly considering it to be an infrasubspecific form, it has been treated as a subspecies name in citations by a few subsequent authors before 1985 (Gaede, 1930, p. 163, as “*Satyrus semele* L. *neapolitana* Std.”, 1931, p. 151, as “*Satyrus semele* Linné var. *neapolitana* Stauder”; Varin, 1960, p. 16, as “*Hipparchia semele* L. ssp. *neapolitana* Staud.”); therefore, in compliance with Article 45 (f, g) of ICZN, it is available and valid. As only *H. senthes* seems to occur on Monte Faito (Kudrna, 1984 ; Kudrna & Leigh, 1988 ; Cesaroni *et al.*, 1994 ; Balletto, Gallo, Jutzeler & Thomson, pers. comm. ; Olivier, pers. obs. July 1991, reported variously as “*neapolitana*” or “*ballettoi*”), we have examined Stauder’s specimens collected **before** 1921 (the date of publication of his *neapolitana* is 30.IV.1921) and designate here 1 ♂ as lectotype and a further 3 ♂, 4 ♀ as paralectotypes. Dissection of the genitalia of the lectotype (illustrated here on text fig. 30) confirmed its identity as *H. senthes*. Hence, Kudrna (1977) erroneously synonymized *neapolitana* under *H. semele semele* and unnecessarily described *Hipparchia ballettoi* in 1984 : the latter name quite correctly was sunk as a junior subjective synonym of “*Hipparchia neapolitana* (Stauder, 1921)” by Jutzeler & de Bros (1997 ; see also Jutzeler *et al.*, 1997). Verity (1923–1924[1924]) confused the matter completely, stating (p. 25) : “Stauder, too (*Zeit. wissen. Insektenbiol.*, 1916, p. 59), is not correct when he refers his *semele* of

Sorrento (...) to *blachieri* or a transition to it; they, of course, are *paeninsulitaliae* and thus, if anything, they point distantly to *mersina*, and on the underside rather to *siciliana*, on account of the light gray tinge of the suffusion". Subsequently, Verity (1953b) listed it as "*Hipparchia (Hipparchia) semele* L. *eserge semele* L. *razza apenninigena* Vrty. *sottorazza paeninsulitaliae* Vrty forma *neapolitana* Stauder". Both Verity's names are junior subjective synonyms of *H. semele*, as correctly established by Kudrna (1977). Being influenced by de Lattin (1949) but, at the same time, apparently completely misled by Verity (1923–1924, 1953b), Varin (1960), as we have seen, considered *neapolitana* to be a subspecies of *H. semele*, but transferred *paeninsulitaliae* to a subspecies of *H. aristaeus* (!), in which he was slavishly followed by Leestmans (1965, 1968). Later on, it was reported from S. (or SW.) Italy as either "*Hipparchia aristaeus aristaeus*" (Higgins & Riley, 1970), "*H. aristaeus*" (D'Abbrera, 1992), "*H. aristaeus siciliana*" (Higgins, 1975) or "*H. aristaeus blachieri*" (Parenzan, 1980; Higgins & Hargreaves, 1983; Higgins & Riley, 1984). Leraut (1997) lists *neapolitana* as a synonym of *Hipparchia semele cadmus* (Fruhstorfer, 1908). Nearly all authors since Kudrna (1984) have listed it as "*Hipparchia ballettoi*" (Balletto & Kudrna, 1985; Sbordonì & Forestiero, 1985; Kudrna, 1986, 1996; Kudrna & Leigheb, 1988; Taymans, 1989; Balletto *et al.*, 1990; Prola & Prola, 1990; Balletto, 1992, 1995; Meyer, 1993; Cesaroni *et al.*, 1994 (rightly noting, however, on p. 114: "*neapolitana* (Stauder, 1921) (type locality: Monte Faito) may represent a senior synonym of *ballettoi*. Examination of Stauder's type material is necessary to establish the correct name for this taxon."); Balletto & Cassulo, 1995; Hesselbarth, van Oorschot & Wagener, 1995 (incorrectly stating, on p. 900: "*ballettoi* Kudrna, 1984 (= *blachierioides* Stauder, 1921", see below); Dennis, Shreeve & Williams, 1995; Munguira, 1995; Jutzeler, Grillo & de Bros, 1995; Dennis, 1997), but De Prins & Iversen (1996) newly downgraded it as "*Hipparchia aristaeus ballettoi*". As we consider the Monte Faito population to be conspecific with those from the Balkans, the Aegean islands and Turkey, *senthes* becomes the oldest available name with both *neapolitana* and *ballettoi* as junior subjective synonyms.

General inference. Initially, we were inclined to consider the Italian populations (Sicily, Monte Faito, Íschia, Capri) as a distinct taxon when compared to *senthes* from the Balkans, the Aegean islands and Turkey, because of (nearly) constant differences in wing markings. The subsequent discovery of a rich colony at Cerenzia (La Sila) yielded material that included all stages in the expression of the wing markings from "true *senthes*" to "*blachieri*". When comparing all Italian material

we have now in our possession, we at best note a clinal pattern of increase in the development, expression and colour intensification of the wing markings towards the Tyrrhenian coast: such an extreme development is also observed in other *Parahipparchia* taxa on some Tyrrhenian islands (*H. aristaeus*, *H. leighebi*, *H. sbordonii*), as well as in some other, more distantly related satyrine butterflies (e. g. *Hipparchia neomiris* (Godart, 1822), *Maniola nurag* (Ghiliani, 1852) and *Lasiommata paramegaera* (Hübner, [1824])) and is thus probably adaptively shaped by selective processes rather than following phylogeny, as already suggested by Cesaroni *et al.* (1994). Olivier & De Prins (1989) demonstrated significant clinal variation in the expression of various wing markings in *Hipparchia mersina*, also assuming that selection is involved. Structural characters (genitalia, androconia) also failed to reveal any discrete property of the Italian populations: to the contrary, if anything were worthy of further investigation in this respect, it would rather be a biometric study of the male genitalia in the various Anatolian populations. What we know of the bionomics of this species throughout its range does not allow us to retain anything in support of a taxonomic differentiation of any population. Therefore, we logically conclude that, when considering all known populations of *H. senthes* throughout its known range, there is no present evidence supporting a breakdown of this species into smaller taxonomic — not even subspecific — units. It is self-evident that a test of our conclusions by other means, especially molecular techniques, would be most revealing. We treat *H. senthes* as a full species when compared to the other three recognized *H. aristaeus* group taxa, because of its total geographical isolation, combined with a distinct habitat specialization, and its significant morphological and allozyme differentiation (Cesaroni *et al.*, 1994 present data for “*H. ballettoi*” (Monte Faito) that convincingly support its species status when compared to *H. algerica*, *H. aristaeus* and all further *Parahipparchia* taxa considered in that study). Direct observations of syntopic and synchronous occurrence of *H. senthes* with *H. semele*, *H. mersina*, *H. volgensis* and *H. pellucida* (vide supra) further corroborate their specific distinctness.

6. On the taxonomic status of “*Satyrus semele* L. f. *blachierioides*” Stauder, 1921

The recorded sympatry of *H. semele* and *H. senthes* in Aspromonte (Calabria) made it a priori not impossible that the taxon described as “*Satyrus semele* L. f.n. *blachierioides*” by Stauder (1921) could refer to *H. senthes*, as suggested by Hesselbarth, van Oorschot & Wagener



Fig. 31. Lectotype of *Satyrus semele* L. f. *blachierioides* Stauder, 1921 [= *Hipparchia semele* (Linnaeus, 1758)]: genitalia (specimen illustrated on plate 2, fig. 6).

(1995) and Jutzeler *et al.* (1997), albeit under the respective names “*ballettoi*” and “*neapolitana*” (vide supra, section 5.4). As, in Stauder’s (1921) publication, *blachierioides* is quoted first on the same page as *neapolitana* (p. 29), it would have been, in that case, the valid name for the south Italian population if it deserved a name on its own. Despite the fact that Stauder (1921) published the name *blachierioides* for “die dunklere, trübere südkalabrische Montanunterrasse aus dem Aspromonte”, i. e. as an infrasubspecific name (“mountain subrace”), it has subsequently been treated as a subspecies name in citations by Gaede (1930, 1931), de Lattin (1949) and Varin (1960 : the latter author inexplicably listing it as a subspecies from Austria!) and is thus, in compliance with Article 45 (f, g) of ICZN, available and valid. We therefore have examined Stauder’s specimens collected **before** 1921 (the

date of publication of his *blachierioides* is 30.IV.1921) and designate here 1 ♂ as lectotype (illustrated on plate 2, fig. 6 of the present study) and a further 5 ♂, 1 ♀ as paralectotypes. Dissection of the genitalia of the lectotype (illustrated here on text fig. 31) confirmed its identity as *H. semele*, hence this name does not apply to any *Hipparchia aristaeus* group taxon and it will not be dealt with further in the present study. The following synonymy is confirmed :

“*Papilio Nymphalis Semele*” Linnaeus, 1758. — Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, Cum Characteribus, Differentiis, Synonymis, Locis. Tomus I, Editio Decima, Reformata : 474. Locus typicus restrictus : S. Sweden (Kudrna, 1977 : 63). Type material : lectotype ♀, in coll. Linnean Society of London ; design. Kudrna (1977 : 63).

“*Satyrus semele* L. f.n. *blachierioides*” Stauder, 1921. — *Dt. ent. Z. Iris* 35 : 29. Locus typicus : Aspromonte. Type material : lectotype ♂, paralectotypes 2 ♂, 1 ♀, in The Natural History Museum, London, 3 ♂, in Narodni Prirodovedecke Museum (National Natural History Museum) Prague ; design. here Olivier & Coutsis. — Junior subjective synonym of *Papilio Nymphalis Semele* Linnaeus, 1758 (Kudrna, 1977 : 60).

“*Satyrus semele blachierioides*” Gaede, 1930. — Satyridae [part.]. In : Seitz, A. (Ed.) : Die Gross-Schmetterlinge der Erde. Eine systematische Bearbeitung der bis jetzt bekannten Gross-Schmetterlinge I. Supplement 1 : 163. — Subsequent misspelling of the name *blachierioides* Stauder, 1921 (see also Verity, 1953b : 310, 311, 340 ; Varin, 1960 : 16 ; Kudrna, 1977 : 60 and Leraut, 1997 : 191).

“*Hipparchia neapolitana* (...) forme *blachierioides*” Jutzeler, Biermann, Hesselbarth, Russo, Sala & de Bros, 1997. — *Linn. belg.* 16 : 118. — Subsequent misspelling of the name *blachierioides* Stauder, 1921.

7. Characters that could be useful for constructing a cladogram of *Parahipparchia*

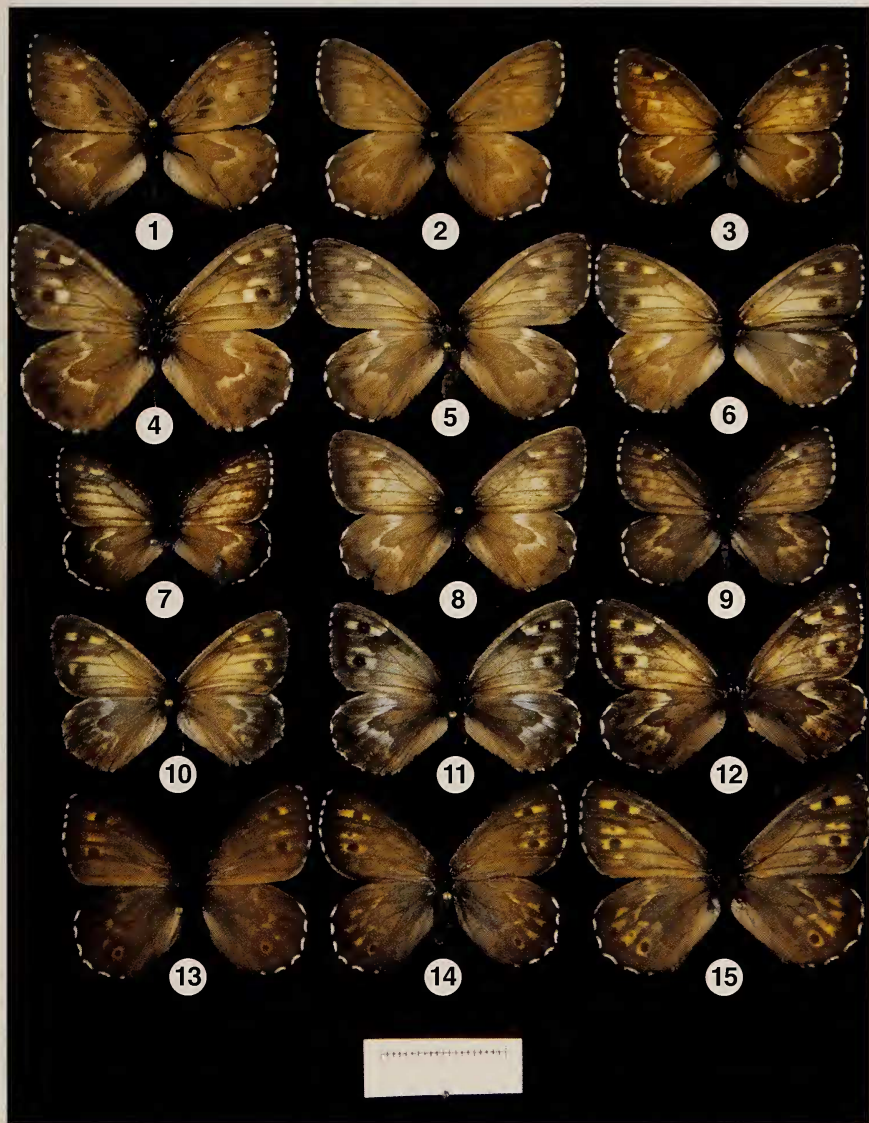
The only attempt so far at constructing a cladogram of *Parahipparchia* has been made by Balletto *et al.* (1990). A first examination of it reveals that in both theirs and our own study *azorina*, *occidentalis* (reported as “*caldeirensis*” [sic!]) and *miguelensis* come out as a monophyletic group. In their study, the *Hipparchia aristaeus* group is treated as monophyletic as well, based on two putative synapomorphies that we have not been able to corroborate (see section 5 and below). Furthermore, the proposed interrelationship of the taxa within this group is

not in agreement with our results : *H. aristaeus* and *H. senthes* are positioned much closer to each other than either one is to "*H. blachieri*" or "*H. ballettoi*".

Cesaroni *et al.* (1994), studying evolutionary relationships among part of the known *Parahipparchia* taxa, also obtained conflicting results when compared to those of Balletto *et al.* (1990), which made them conclude categorically (p. 113) : "As one example, their parsimony tree based on morphological characters puts two well-separated species, *H. aristaeus* and *H. algirica*, closer than the conspecific, allozymically identical, *H. s. semele* and *H. s. wilkinsoni*. This kind of bias is probably

Plate 3. Superspecies *Hipparchia azorina*.

1. *Hipparchia (azorina) azorina azorina* (Strecker, 1899) ♂. Portugal, Azores, Pico, Chã do Pelado (800 m), 15.VIII.1990, leg. M. Meyer, in coll. VLCA.
2. *Hipparchia (azorina) azorina azorina* (Strecker, 1899) ♂. Portugal, Azores, Faial, Gordo (1000 m), 10.VIII.1982, leg. J. Demange, in coll. VLCA.
3. *Hipparchia (azorina) azorina occidentalis* Bivar de Sousa, 1982 ♂. Portugal, Azores, Flores, Caldeira Funda, 29.VIII.1986, leg. E. Balletto, in coll. VLCA.
4. *Hipparchia (azorina) azorina azorina* (Strecker, 1899) ♀. Portugal, Azores, Pico, Tronqueira (850 m), 14.VIII.1982, leg. J. Demange, in coll. VLCA.
5. *Hipparchia (azorina) azorina azorina* (Strecker, 1899) ♀. Portugal, Azores, Faial, Gordo (1000 m), 10.VIII.1982, leg. J. Demange, in coll. VLCA.
6. *Hipparchia (azorina) azorina occidentalis* Bivar de Sousa, 1982 ♀. Portugal, Azores, Flores, Caldeira Comprida (580 m), 8.VIII.1990, leg. M. Meyer, in coll. VLCA (genitalia illustrated on text fig. 8B).
7. *Hipparchia (azorina) azorina occidentalis* Bivar de Sousa, 1982 ♂. Portugal, Azores, Flores, Caldeira Funda, 29.VIII.1986, leg. Balletto, in coll. VLCA.
8. *Hipparchia (azorina) azorina occidentalis* Bivar de Sousa, 1982 ♂. Portugal, Azores, São Jorge, Serra do Topo, Pedra Vermelha (800 m), 17.VIII.1990, leg. M. Meyer, in coll. VLCA (genitalia illustrated on text fig. 7A).
9. *Hipparchia (azorina) azorina occidentalis* Bivar de Sousa, 1982 ♂. Portugal, Azores, Terceira, Serra de Santa Barbara (1000 m), 17.VII.1994, leg. H. Henderickx, in coll. VLCA.
10. *Hipparchia (azorina) azorina occidentalis* Bivar de Sousa, 1982 ♀. Portugal, Azores, Flores, Caldeira Comprida (580 m), 8.VIII.1990, leg. M. Meyer, in coll. VLCA (genitalia illustrated on text fig. 8A).
11. *Hipparchia (azorina) azorina occidentalis* Bivar de Sousa, 1982 ♀. Portugal, Azores, São Jorge, Serra do Topo, Pedra Vermelha (800 m), 17.VIII.1990, leg. et coll. M. Meyer.
12. *Hipparchia (azorina) azorina occidentalis* Bivar de Sousa, 1982 ♀. Portugal, Azores, Terceira, Serra de Santa Barbara (1000 m), 18.VIII.1990, leg. M. Meyer, in coll. VLCA (genitalia illustrated on text fig. 9B).
13. *Hipparchia (azorina) miguelensis* (Le Cerf, 1935) ♂. Portugal, Azores, São Miguel, Serra de Agua de Pau (900 m), 22.VII.1994, leg. H. Henderickx, in coll. VLCA (genitalia illustrated on text fig. 10A).
14. *Hipparchia (azorina) miguelensis* (Le Cerf, 1935) ♂. Portugal, Azores, São Miguel, Serra de Agua de Pau (900 m), 24.VII.1994, leg. H. Henderickx, in coll. VLCA.
15. *Hipparchia (azorina) miguelensis* (Le Cerf, 1935) ♀. Portugal, Azores, São Miguel, Serra de Agua de Pau (900 m), 24.VII.1994, leg. H. Henderickx, in coll. VLCA (genitalia illustrated on text fig. 11B).





the outcome of a questionable multistate coding of quantitative morphological characters. Thus the conflict between our results based on phenetic algorithms and Balletto *et al.*'s cladistic analysis is not due to a conflict of methodologies, but rather due to the selection and coding of characters”.

In the present section, we will list a series of adult characters of potential use for constructing a cladogram of *Parahipparchia* and we will review the 27 multistate characters listed by Balletto *et al.* (1990): these last ones will be dealt with at their appropriate place in the following discussion, being enumerated as “B” followed by the number given to it in their publication (on p. 172, table 2b). For ease of use in future phylogenetic work, each character will be coded as binary, “a” being the supposed plesiomorphous state and “b” the supposed apomorphous state. While Balletto *et al.* (1990) list only structural characters (androconial scales and genitalia), we include also wing characters. For determining the polarity of characters, we have applied the methodology of outgroup comparison. The outgroup is formed by *Hipparchia s. str.*, the supposed sister-group of *Parahipparchia* (cf. García-Barros & Martín, 1991); where appropriate, it will be extended to include the whole Satyriti *sensu* Harvey (1991): when this is the case, it will be stated explicitly. For definitions on phylogenetic terminology see Appendix.

WING CHARACTERS

1. a) Apex forewing \approx rounded

All taxa of *Hipparchia s. str.* and *Parahipparchia* except *H. (azorina) miguelensis*

Plate 4. *Hipparchia aristaeus* group.

1. *Hipparchia maderensis* (Baker, 1891) ♂. Portugal, Madeira, Curral das Freiras (600–700 m), 24.VII.1993, leg. A. Olivier, in coll. VLCA.

2. *Hipparchia maderensis* (Baker, 1891) ♀. Portugal, Madeira, 2 km SW. Poiso (1350 m), 25.VII.1993, leg. A. Olivier, in coll. VLCA.

3. *Hipparchia algerica* (Oberthür, 1876) ♂. Morocco, Middle Atlas, Tizi-n-Tretten (1950 m), 27.VI.1994, leg. A. Olivier, in coll. VLCA.

4. *Hipparchia algerica* (Oberthür, 1876) ♀. Morocco, Middle Atlas, Ifrane (1650 m), 24.VI.1994, leg. A. Olivier, in coll. VLCA.

5. *Hipparchia aristaeus* (Bonelli, 1826) ♂. Italy, Sardinia, Prov. Nuoro, Monti del Gennargentu, 12 km SE. Fonni (500 m), 22.VII.1992, leg. A. Olivier, in coll. VLCA.

6. *Hipparchia aristaeus* (Bonelli, 1826) ♀. Italy, Sardinia, Prov. Nuoro, Monti del Gennargentu, 4 km S. Fonni (1000 m), 25.VII.1992, leg. A. Olivier, in coll. VLCA.

7. *Hipparchia synthes* (Fruhstorfer, 1908) ♂. Greece, Eastern Aegean islands, Híos, Kambiá (150 m), 20.VI.1990, leg. A. Olivier, in coll. VLCA.

8. *Hipparchia synthes* (Fruhstorfer, 1908) ♀. Greece, Eastern Aegean islands, Ikaría, Oxéa (450 m), 8.VI.1990, leg. A. Olivier, in coll. VLCA.

b) Apex forewing distinctly pointed
H. (azorina) miguelensis (autapomorphy)

2. a) Outer margin forewing \approx straight
All taxa of *Hipparchia s. str.* and *Parahipparchia* except *H. (azorina) miguelensis* and *H. sbordonii* pro parte

b) Outer margin forewing convex
H. (azorina) miguelensis and *H. sbordonii* pro parte

As we found no other character shared only by *miguelensis* and *sbordonii* and their placement in distinct groups within *Parahipparchia* is supported by several synapomorphies for each of them, character state 2b represents a case of parallelism and hence an autapomorphy of each one.

3. a) ♀ upperside forewing basal and discal area of the same ground-colour as remainder of wing

All taxa of *Hipparchia s. str.* and, within *Parahipparchia*, both the *H. aristaeus* and *H. semele* species groups

b) ♀ upperside forewing basal and discal area lighter brown-grey to creamy white

Superspecies *H. azorina* (synapomorphy)

This character could be of some use in the males as well: state a is occurring in the same groups as for the females, plus invariably in *H. (azorina) miguelensis* and usually in *H. (azorina) azorina*; state b is occurring invariably in *H. (azorina) azorina occidentalis*, but only occasionally in *H. (azorina) azorina azorina*. If completed by the qualification "potentially" for the males, it could perhaps be considered as a synapomorphy of both last-mentioned taxa (or as an autapomorphy of *H. (azorina) azorina*).

4. a) Sex brand normally developed

All taxa of *Hipparchia s. str.* and, within *Parahipparchia*, both the *H. aristaeus* and *H. semele* species groups

b) Sex brand vestigial or absent

Superspecies *H. azorina* (synapomorphy)

5. a) Sex brand vestigial, but always at least traces of it

H. (azorina) miguelensis and *H. (azorina) azorina azorina*

b) Sex brand absent, although scattered androconial scales may be present

H. (azorina) azorina occidentalis (autapomorphy)

A sex brand is always well developed in *Hipparchia s. str.* and, within *Parahipparchia*, in both the *H. aristaeus* and *H. semele* species groups: it is always "complete" in its development, although it may be somewhat

reduced in extent, as e. g. in *H. pellucida cypriensis*. This appears also to be the case in e. g. *H. hansii* (Austaut, 1879) (*Neohipparchia*) and *H. tewfikii* (Wiltshire, 1949) (*Pseudotergumia*). Only in superspecies *H. azorina* is there a progressive disappearance of the sex brand. Outside *Hipparchia s. l.* the sex brand can be either well developed or completely absent within the same genus, e. g. in *Satyrus*. Having noticed that, in both *H. maderensis* and *H. aristaeus*, the sex brand often extends well into s1a, we have looked for this condition in both *Hipparchia s. str.* and in *Parahipparchia*: in the former we found it in *H. alcyone* ([Denis & Schiffermüller], 1775), in the latter in *H. mersina*. Therefore, it would seem unwise to us to list it as a possible synapomorphy of *H. maderensis* + *H. aristaeus*.

6. a) Upperside hindwing submarginal area consisting of either a more or less complete series of orange-ochreous patches in s2–s5(6), interrupted by veins (*Parahipparchia* except *H. (azorina) azorina*, *H. hansii* (!), *Arethusana*, some *Oeneis*) or a continuous, uninterrupted band (*H. neomiris* (!), most *Pseudochazara*, some *Karanasa*)
- b) Upperside hindwing submarginal area unmarked, being part of the groundcolour
H. (azorina) azorina, remainder of the Satyriti

This character is probably useless at a level higher than *Parahipparchia* and it appears even impossible to determine its polarity. Within *Parahipparchia*, however, character state 6b is restricted to *H. (azorina) azorina*, while, interestingly, *H. (azorina) miguelensis* has condition 6a, as does the remainder of *Parahipparchia*. Therefore, the loss of the submarginal markings in *H. (azorina) azorina* is likely to be secondary and hence an autapomorphy of this taxon (or a “synapomorphy” of both subspecies *azorina* and *occidentalis*).

At this point we would like to mention that García-Barros & Martín (1991) list one character (no. 51 in their study) as a possible synapomorphy of *Hipparchia s. l.*, i. e. “Hindwing underside with inner margin postdiscal band forming a notch at the level of veins M2–M3”. While this is clearly the case with *Parahipparchia* (and other subgenera of *Hipparchia*, as for instance in *Pseudotergumia*), its expression is far less convincing in several *Hipparchia s. str.* taxa, while it sometimes is quite apparent outside *Hipparchia s. l.*, e. g. in males of *Pseudochazara anthelea* (Hübner, [1824]). Therefore, we are sceptical about its usefulness as a synapomorphy of *Hipparchia s. l.*

ANDROCONIAL SCALES

7. a) Androconium neomorphic

When androconial scales are present, this is the condition in all Satyriti, except some *Karanasa* and all *Parahipparchia* but one (*H. mersina*)

b) Androconium eomorphic/palaeomorphic

Parahipparchia except *H. mersina*, some *Karanasa*

While the usefulness of this character (= B1, condition in *H. mersina* listed there as “paleo[morphic]/neom.[orphic]”) could be questioned at some higher level in the Satyriti, and certainly when other subtribes of the Satyrini sensu Harvey (1991) are also considered (vide supra, section 1.2), it appears informative at the level of *Parahipparchia*. Character state 7b is a synapomorphy of *Parahipparchia*, while the re-appearance of 7a in *H. mersina* is a reversal of character state and, being secondary, an autapomorphy of that species.

As can be seen from the present study, androconial scales can be of some use as diagnostic features of a few nominal taxa within *Parahipparchia*, but their value for phylogenetic purposes, at least as far as superspecies *H. azorina* and the *H. aristaeus* group are concerned, appears very limited. B2 (length), consisting of six states (the seventh being “absent”), includes three states that apply to taxa treated in the present study, i. e. “normal” (*miguelensis*, “*ballettoi*”, “*blachieri*”, *aristaeus* and *senthes*), “short” (*azorina*, *algerica*, *maderensis*) and “long” (“*caldeirensis*” [sic! recte *occidentalis*]), while the state “absent” is attributed to *sbordonii*: in the latter case, “*caldeirensis*” and *sbordonii* have been switched mistakenly. The other taxa seem more or less well placed in their respective categories, except *senthes* (with “*ballettoi*” and “*blachieri*”), which possesses scales that could, taking the marked individual variation into account, be ascribed to either of the two first categories. As our own analysis of this character for the whole subgenus has not been completed yet, we will not comment further on this issue here, but we do not expect too much from future results in this field. B3 (apex with or without terminal filament) is a duplicate of [part of] B1 and thus adds no useful information.

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B4 (overall size). Five categories have been distinguished, for which we can agree only with the attribution of taxa to the category “smallest” (*azorina*, *miguelensis* and “*caldeirensis*”). All *Hipparchia aristaeus* group taxa are brought under into the category “average”, along with

sbordonii and the outgroup taxon *H. fagi* (Scopoli, 1763) — both of which have, in fact — very large genitalia. *H. turcmenica*, which has genitalia very similar to those of *H. pellucida*, is mistakenly placed in a category “very small”, while the latter taxon is placed in the category “largest”: in this species, the overall size of these structures can indeed be very large (Caucasus). Furthermore, overall size can vary considerably within a single species, e. g. *H. mersina* (Olivier & De Prins, 1989). Thus, this character does not seem very well suited for our purpose.

B5 (thickness). Three states are distinguished, i. e. “normal”, “stout” and “slender”. Of the taxa considered in the present study, *miguelensis*, *algerica*, *maderensis*, “*ballettoi*”, “*blachieri*” and *aristaeus* are placed in the first category, while *azorina*, “*caldeirensis*” and *senthes* are placed in the second category. Curiously, *H. senthes* as we now understand it, is placed in two distinct categories. However, as it is not clear what the authors exactly mean by “thickness”, we have difficulties in understanding what could be the value of this “character”.

B6 (uncus : length). Five categories have been distinguished. Of the taxa considered in the present study, *azorina* and “*caldeirensis*” are placed in the fifth category ($<$ tegumen), while *miguelensis*, *algerica*, *maderensis*, “*ballettoi*”, “*blachieri*”, *aristaeus* and *senthes* are brought into the fourth category ($=$ tegumen). It is true that in *H. (azorina) azorina*, we found the uncus to be shorter than the tegumen in twelve out of fifteen specimens (one specimen from Flores and from São Jorge, however, had LUN/LT1 values of resp. 1.02 and 1.03). In *H. (azorina) miguelensis* and in the *H. aristaeus* group, the uncus is never shorter than the tegumen, with values between 1.05 and 1.20 (in *senthes* between 1.10 and 1.36). In *Hipparchia s. str.*, the uncus is always longer than the tegumen, though in *H. fagi* both structures can be of almost equal length. In that subgenus, values are found that overlap largely with those of the *H. aristaeus* group and *miguelensis*. Therefore, beside the fact that category D (uncus = tegumen) does not correspond exactly to reality, the condition in this group is plesiomorphic anyway. Category E (uncus $<$ tegumen) is not found in every *azorina* specimen and therefore we do not consider it to be a useful apomorphy. Furthermore, the uncus is invariably shorter than the tegumen in *Neohipparchia*, *Euhipparchia* and *Pseudotergumia*, making the potential value of this character state even more questionable. In the *H. semele* group, the uncus tends to become much longer than the tegumen, but there can be considerable intraspecific (geographic) variation in this feature : in *H. mersina*, for instance, LUN/LT1 can

vary from 1.28 (Greece : Lésvos) to 2.10 (Turkey : Prov. Adana) (Olivier & De Prins, 1989) and in *H. semele* such tendencies exist as well, though not to such an extent (Olivier & Coutsis, unpublished data). There is also overlap in values with *Hipparchia* s. str., although these tend to be very high in some *H. semele* group taxa, like *leighebi*, *sbordonii*, *cretica* and *christenseni*. For these reasons we do not consider this character to be reliable for phylogenetic analysis.

B7 (uncus : shape) and B8 (uncus : apex). For both these characters, Balletto *et al.* (1990) considered four states. We found it impossible to quantify these characters into the discrete categories distinguished by these authors, because of the considerable degree of variation within some species (e. g. *H. mersina*, cf. Olivier & De Prins, 1989). Furthermore, in the *H. aristaeus* group, for instance, the uncus is not thicker than, say, in *H. semele* or *H. "malickyi"* (the latter is a junior subjective synonym of *H. mersina*, cf. Olivier & De Prins, 1989) : this impression of thickness may just be due to the fact that these taxa have a shorter uncus. We will not consider these characters further in our analysis.

B9 (brachia [length]). Again, four states were listed. According to Balletto *et al.* (1990), in "*caldeirensis*", the brachia [termed gnathos throughout the present study] is more or less equal in length to the uncus. The three males from Flores that we examined do not appear to show the proposed character state. *H. mersina* and *H. "malickyi"* are placed in a category "brachia \ll uncus", a result quite different from that of Olivier & De Prins (1989). The gnathos tends to be comparatively shorter than the uncus in *H. algerica* and *H. aristaeus*, but not so much as to justify a discrete category, and *H. senthes* is certainly not well placed in it. In general, the length of the gnathos is, like that of the uncus, subject to allometric growth. We therefore reject it as a reliable character for phylogenetic analysis.

B10 and B11 (brachia [shape]). The longer the gnathos, the more curved it is. Therefore, the distinctions proposed by Balletto *et al.* (1990) are an artefact. The relative thickness of the gnathos is correlated to that of the uncus. We therefore do not consider these characters reliable for similar reasons as we do with B6, B7 and B9.

B12 (phallus [shape]). The aedeagus tends to be more or less straight in superspecies *H. azorina*, while it appears more curved in the remainder of *Parahipparchia*. We have been unable to confirm Balletto *et al.*'s (1990) finding that the straight condition also appears to be diagnostic for *volgensis*, "*delattini*", *christenseni* and *cypriensis*, at least

on a constant basis. In *Hipparchia s. str.* (and, we must say, in *Parahipparchia* as well), we found both conditions to exist, while it is sometimes impossible to ascribe unambiguously an observed case to one of both character states. Therefore, this character seems unlikely to be of any use for phylogenetic work with this group.

B13 (phallus [length]). Not surprisingly, the penis is, in absolute length, smaller in superspecies *H. azorina* than in the remainder of *Parahipparchia* (see also B4). In all the taxa revised in the present study, the penis is invariably longer than uncus + tegumen. According to Balletto *et al.* (1990), however, it should be shorter in *H. aristaeus* and *H. senthes*, and more or less equal in "*ballettoi*". We have not investigated this situation thoroughly in each single *Parahipparchia* taxon, but in *H. mersina* the penis is indeed shorter than uncus + tegumen, with only one single specimen being the exception (Olivier & De Prins, 1989). This suggests that the penis could be less subjected to allometric growth than is the case with the uncus and the gnathos. In Italian *H. semele*, *H. leighebi* and *H. sbordonii*, the penis appears to be either slightly shorter or slightly longer than uncus + tegumen. In *Hipparchia s. str.*, the penis always seems to be longer than uncus + tegumen. In view of these data, the validity of this character for phylogenetic analysis appears quite questionable: in any case, its state in both superspecies *H. azorina* and in the *H. aristaeus* group would appear plesiomorphic.

B14 (phallobase). Balletto *et al.* (1990) recognize two categories: A (broad) and B (narrow): the whole *H. semele* group except *H. christenseni* is placed in the first group; last-named species, superspecies *H. azorina* and the *H. aristaeus* group, as well as *H. fagi*, are placed in the second group. We have been unable to confirm any such distinction in the phallobase among *Parahipparchia* taxa and, consequently, we cannot view this as a reliable character for phylogenetic analysis.

8. a) Aedeagus without any spines

All *Hipparchia s. str.* taxa and, within *Parahipparchia*, both the *H. aristaeus* and *H. semele* species groups

b) Aedeagus dorsally with small spines in its distal half

Superspecies *H. azorina* (synapomorphy)

It must be said that, in the Satyriti, small spines on the aedeagus have been found as well in *Berberia* (Le Cerf, 1914) and *Satyrus* (Nekrutenko, 1985, 1990). As, however, in *Hipparchia s. l.* these are present only in superspecies *H. azorina*, they certainly represent an informative and useful character at this level.

9. a) Valve with well developed dorsal process
Hipparchia s. l., except taxa listed under b)
b) Valve with dorsal process reduced or (nearly) absent
H. turcmenica, *H. christenseni*, *H. pellucida*, most *H. volgensis*
(synapomorphy)

H. volgensis is quite variable in this respect : some populations (e. g. Óros Helmós) have a well developed dorsal process, as is invariably the case in this (sub-)genus, except for the taxa listed under b), while other populations have a reduced dorsal process, approaching the condition in *turcmenica* and *pellucida*. Balletto *et al.* (1990) consider three categories, whereby the “upper process” is considered to be rudimentary in “*hesselbarthi*” and absent in *pellucida* and *cypriensis* : they do not, however, emphasize the reduction of the dorsal process in *volgensis* (with “*muelleri*” and “*delattini*”) and in *christenseni*.

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B16 (signa [shape]). Two states are recognized : straight (*H. fagi*, all *Parahipparchia* taxa except *H. leighebi*) and curved (*H. leighebi*). We have not been able to confirm this distinction.

B17 (signa [size]). Five categories have been distinguished, with which we can agree only to a limited extent. Category E (very long) includes “*ballettoi*” and “*blachieri*” and indeed we found the longest signa in *H. senthes* material from Sicily and S. Italy. Category D (very short) includes *azorina* (and “*caldeirensis*”) : here we would certainly add *miguelensis* and *mersina*. The remainder of the *H. semele* group we would place in category A (average) rather than B (short), while the *H. aristaeus* group is well placed in category C (long). It seems impossible, however, to interpret these data phylogenetically, except for one category (i. e., D : very short ; see below), as values corresponding to those encountered in the majority of taxa in both *H. aristaeus* and *H. semele* groups have also been found in *Hipparchia s. str.* (Coutsis, 1984 ; Coutsis & Olivier, unpublished data).

10. a) Average signum length > 1.50 mm
Hipparchia s. str., *Parahipparchia* except superspecies *H. azorina*
b) Average signum length < 1.50 mm
Superspecies *H. azorina* (synapomorphy)

In superspecies *H. azorina*, the signum is distinctly shorter on average than in any other taxon of both *Hipparchia s. str.* and *Parahipparchia*, but there is little overlap in absolute length with some *H. mersina* specimens (cf. Olivier & De Prins, 1989). As there is no further evidence for a possible sister group relationship between superspecies *H. azorina*

and *H. mersina*, it may be assumed that character state 10b is a synapomorphy of superspecies *H. azorina*, while the condition in *H. mersina* (n = 59, average = 1.57, calculated after Olivier & De Prins, 1989: 214–215, table 7) could be regarded as an autapomorphy of that species.

B18 (corpus bursae [size]). We investigated this character in all taxa revised in the present study, as well as in several *H. semele* group and *Hipparchia s. str.* taxa. Balletto *et al.* (1990) distinguished five classes: we agree with their attribution of superspecies *H. azorina* to the category “very small” and of *H. mersina* to the category “small”, while *fagi*, *algerica*, *maderensis*, *aristaeus* and *senthes* are well placed in the class “large” and “*blachieri*” (i. e. Sicilian *senthes*) indeed has the largest corpus bursae in *Parahipparchia*. We did, however, find similar values as for the *H. aristaeus* group in *H. sbordonii* and, partly, *H. leighebi* and *H. semele* from Calabria and Sicily. Furthermore, we do not agree with the attribution of “*ballettoi*” to the category “normal” and that of “*malickyi*” to the category “large”. Because of overlap with *Hipparchia s. str.* in both the *H. aristaeus* and *H. semele* groups, we cannot support the postulated value of this character for phylogenetic work, at least the way it is presented by these authors. It is, however, possible to consider the following character for our purpose.

11. a) Average length of corpus bursae > 2.50 mm
Hipparchia s. str., *H. aristaeus* and *H. semele* groups
- b) Average length of corpus bursae < 2.50 mm
Superspecies *H. azorina* (synapomorphy)

Single specimens of *H. mersina* may have a corpus bursae as small as that of *miguelensis*, but on average it remains distinctly larger in the former species.

B19 (corpus bursae [distal end: sic! recte cervix bursae]). Three categories have been distinguished, viz. “little sclerotized”, “sclerotized” and “very sclerotized”. It is true that superspecies *azorina*, as well as *semele*, *leighebi* and *sbordonii*, has a little sclerotized cervix bursae, as is the case with *Hipparchia s. str.* (Coutsis, 1984; Coutsis & Olivier, unpublished data). The sclerotization is, as a rule, more pronounced in the *H. aristaeus* group (including “*ballettoi*”!) and in *H. cretica* (Coutsis, 1984; this study), and even more in *mersina*, *volgensis*, *christenseni*, *turcmenica* and *pellucida* (Coutsis, 1984; Olivier & De Prins, 1989). This could be interpreted as a synapomorphy of the *H. aristaeus* group and last-named six taxa of the *H. semele* group. As this contradicts the monophyly of the *H. semele* group that is well supported by other characters, we believe that this condition (more

heavily sclerotized cervix bursae) is homoplasous. Assuming that this condition originated at least twice, and excluding the *H. semele* group taxa, one would be inclined to list it as a synapomorphy of the *H. aristaeus* group. Considering the presumably homoplasous nature of the character and, not least, the degree of intraspecific (individual) variation in its expression, we seriously doubt its potential value as a reliable character for the present purpose. We found, however, another character state that we consider useful for phylogenetic work.

12. a) Cervix bursae relatively narrow and flat, little to moderately sclerotized

Hipparchia s. str., superspecies *H. azorina*, *H. aristaeus* group, *H. semele*, *H. leighebi*, *H. sbordonii*, *H. cretica*

b) Cervix bursae distinctly broader, often cup-shaped and moderately to heavily sclerotized

H. mersina, *H. turcmenica*, *H. volgensis*, *H. christenseni*, *H. pellucida* (synapomorphy)

This character is useless for our analysis of both superspecies *H. azorina* and the *H. aristaeus* group, but it appears informative for part of the *H. semele* group. Coutsis (1984) studied only two females of *H. mersina*: the condition reported in that study is quite atypical for that species (cf. Olivier & De Prins, 1989).

B20 (ductus bursae [degree of sclerotization]). Balletto *et al.* (1990) report it as "sclerotized" in *H. algerica*, *H. maderensis*, *H. "blachieri"*, *H. aristaeus* and *H. senthes*, and as "little sclerotized" in all other *Parahipparchia* taxa (including *H. "ballettoi"*!) as well as in *H. fagi*. We found the ductus bursae to be indeed more sclerotized in the *H. aristaeus* group in general, but there is quite some variation in the degree of sclerotization. *H. senthes* from S. Italy does not appear to differ markedly from the other taxa of this group in this respect. It would be tempting to consider this character state as a synapomorphy of the *H. aristaeus* group, but this appears not to be the case. Some specimens of *H. senthes*, for instance, show hardly any difference in this respect from some *H. semele* specimens. The degree of sclerotization in *H. mersina* appears to vary substantially individually: in most specimens the ductus bursae is membranous or weakly sclerotized, but in some specimens it is well sclerotized, much as in the *H. aristaeus* group taxa (cf. Olivier & De Prins, 1989). Exceptionally, such may even be the case with *H. volgensis* from Greece (Olivier & De Prins, unpublished data). We are therefore compelled to discard the present character as well.

13. a) Bend of ductus bursae prominent and well separated from cervix bursae

Hipparchia s. str., superspecies *H. azorina*, *H. aristaeus* group, *H. semele*, *H. sbordonii*, *H. leighebi*

b) Bend of ductus bursae less prominent to imperceptible, highly compressed against cervix bursae

H. cretica, *H. mersina*, *H. volgensis*, *H. turcmenica*, *H. christenseni*, *H. pellucida* (synapomorphy)

Balletto *et al.* (1990) recognize three character states, viz. “prominent”, “compressed” and “very compressed” and Coutsis (1984) makes a similar distinction. Their first category corresponds exactly to our character state 13a and includes the same taxa as in our study (with some additional ones, that we consider synonymous). Their second category includes *H. mersina*, though, as we have already said while discussing character 12, the specimens dealt with by Coutsis (1984) appear atypical : in most specimens of that species, the bend of ductus bursae is highly compressed against the cervix bursae, much as in *volgensis*, *turcmenica*, *christenseni* and *pellucida*. We would rather place it in their third category, leaving only *cretica* in the second one. As already stated, we code each character as binary, hence *cretica* is also listed under 13b. Again we have here a useless character for superspecies *H. azorina* and the *H. aristaeus* group but, interestingly, the same group — plus *H. cretica* — comes out again as a monophyletic unit.

B22 (bend [of ductus bursae] : prox.[imal] end). Balletto *et al.* (1990) consider four categories : “normal”, “wider”, “narrower” and “inflated”. According to them, “*malickyi*” and *mersina* belong to resp. the first and the third category, *turcmenica* is also placed in the third category, while *cretica* is the only taxon in the category “wider”. The fourth category comprises *H. fagi*, *H. volgensis* (with “*muelleri*” and “*delattini*”) and *H. pellucida*, while *christenseni* surprisingly is put into the first category. All this does not agree with our own observations ; the more, as a matter of fact, the width of the proximal end of the bend of the ductus bursae varies a lot individually and depends entirely on the width of the cervix bursae. For these reasons this character appears not to be adequately defined nor worthy of further consideration.

B23 (ductus bursae [shape]). According to Balletto *et al.* (1990), it is “thin” in all *Parahipparchia* taxa, except *H. pellucida* (with *cypriensis*) that, together with *H. fagi*, has a “thick” one. It is true that it is wider in *H. pellucida* than in any other taxon in both *Parahipparchia* and *Hipparchia s. str.* (including *H. fagi*, that does not differ from the other *Parahipparchia* taxa in this respect). This character appears in fact

to be correlated with character 12 (and, consequently, a duplicate of it). At best, one could consider the state in *H. pellucida* as an autapomorphy of that single taxon, and hence of no use for a reconstruction of the phylogeny of *Parahipparchia*.

B24 (ductus [bursae]: length). There is a rather important variation in the length of the ductus bursae, both interspecifically and intraspecifically; in *Hipparchia* s. str., this structure appears to be very long in *H. fagi* and *H. syriaca* (Staudinger, 1871), but much shorter in, for instance, *H. alcyone* ([Denis & Schiffermüller], 1775) (Coutsis, 1984), while in *Parahipparchia* it is proportionally shorter in *H. pellucida* and hence could perhaps be regarded as an autapomorphy of that species. It is also short in *azorina* (and "*caldeirensis*"), as pointed out by Balletto *et al.* (1990), but this is logical considering the small size of the corpus bursae in this taxon (vide supra, character 11): nevertheless, its length in superspecies *H. azorina* sometimes overlaps with that of *H. maderensis*, *H. algerica* and *H. aristaeus* (in *H. senthes*, the ductus bursae tends to be longer than in the three last-named species). It thus appears that this character is not informative for our purpose.

B25 (sterigma [overall size]). Five categories have been distinguished, which seems very arbitrary to us, the more as there is a relatively important range of variation within each taxon in this respect. It is true that superspecies *H. azorina*, as well as the *H. aristaeus* group, tend to have a smaller sterigma than the *H. semele* group taxa on average, but there is a rather broad range of overlap. As far as we have been able to ascertain, values in *leighebi*, *sbordonii* and *cretica* do always exceed those in both forementioned complexes. In *H. mersina*, Olivier & De Prins (1989) found WST values between 1.97 and 2.78, its lower values covering part of the range of variation of both superspecies *H. azorina* and the *H. aristaeus* group. Interestingly, the taxa within superspecies *H. azorina* do **not** appear to have a smaller sterigma than the *H. aristaeus* group taxa. Within last group, *H. senthes* tends to have a larger sterigma than the other taxa, the highest scores occurring in some Calabrian (La Sila) specimens. In *Hipparchia* s. str., *H. fagi* indeed has an exceedingly large sterigma, but in other species like *H. ellena* (Oberthür, 1894) and, especially, *H. neomiris* (Godart, 1822), size is comparable to that in *Parahipparchia* (Coutsis, 1984; Coutsis & Olivier, unpublished data). Consequently, this character does not seem very well suited for our purpose, at least as far as WST is concerned (but see below, characters 14 and 15).

14. a) Average length of dorso-lateral lobe (LDL) > 1.00 mm
Hipparchia s. str., *H. aristaeus* group, *H. semele* group
b) Average length of dorso-lateral lobe (LDL) < 1.00 mm
Superspecies *H. azorina* (synapomorphy)

The dorso-lateral lobe appears to be larger in *H. fagi* than in any other taxon within both *Hipparchia s. str.* and *Parahipparchia*. In some *Hipparchia s. str.* species, however, this structure does not exceed that of some *Parahipparchia* taxa in length (e. g. *H. autonoe* (Esper, [1784]) and *H. neomiris*, cf. Coutsis, 1984; Coutsis & Olivier, unpublished data). It tends to be distinctly smaller in *H. maderensis* and *H. algerica*, but there is overlap with other *Parahipparchia* taxa. In superspecies *H. azorina*, however, it is on average constantly inferior in size and length.

15. a) Average length of dorsal lamella (LL) ≤ 0.7 mm
Hipparchia s. str., superspecies *H. azorina*, *H. aristaeus* group
b) Average length of dorsal lamella (LL) > 0.7 mm
Hipparchia semele group (synapomorphy)

In *Hipparchia s. str.* the dorsal lamella is very small, both in absolute size and in proportion to the entire sterigma. In superspecies *H. azorina*, it is even smaller in absolute size; in this taxon, this condition is entirely correlated to the very small size of the dorso-lateral lobe and therefore we prefer not to consider it as an additional synapomorphy of this superspecies, as it would do nothing more than to duplicate character 14. The dorsal lamella becomes distinctly larger in the *H. semele* group taxa, but there is a slight amount of overlap in absolute length between the *H. aristaeus* group taxa and, for instance, *H. mersina* (cf. Olivier & De Prins, 1989); the average length of this structure, however, is always superior in the *H. semele* group taxa when compared to the remainder of *Parahipparchia* and to *Hipparchia s. str.*

B26 (mid-dorsal process). Balletto *et al.* (1990) qualify this structure as either "elongate flat" (*H. semele* group), "intermediate" (superspecies *H. azorina* and *H. aristaeus* group), "short flat" (none!) and "short grooved" (*H. fagi*). We found two basic types, viz. either broad at base, short and triangular to rounded, or narrow at base, longer and pointed distally: the former condition predominates in superspecies *H. azorina* and in the *H. aristaeus* group and is also found in some *Hipparchia s. str.* taxa like *H. syriaca* and *H. ellena* (Coutsis, 1984), the latter one is the rule in the *H. semele* group. The situation, however, is not that simple and the two types appear to be linked by intermediate stages in several taxa. In *H. senthes* from La Sila, for instance, the mid-dorsal process remains broad at its base, but is moderately long

and distinctly pointed distally. In several specimens of *H. semele* (Sicily, S. Italy), *H. leighebi* and *H. sbordonii*, the mid-dorsal process is narrow at its base and pointed distally, but rather short. Finally, Olivier & De Prins (1989) encountered both types in *H. mersina*, although the latter type predominates largely. For these reasons, we cannot retain this character for a phylogenetic analysis of *Parahipparchia*.

SPHRAGIS

- 16(B27) a) Sphragis absent
All Satyriti except the *H. semele* group
b) Sphragis present
Hipparchia semele group (synapomorphy), but unknown in *H. turcmenica*

The distribution of the sphragis within *Parahipparchia* has already been discussed in detail in section 1.3. The sphragis is indeed constantly large ("carebate") in *cretica*, *christenseni* and *pellucida* (with *cypriensis*), as noticed by Balletto *et al.* (1990), but we found its development to be quite comparable in *semele* from Sicily and Monte Pollino (S. Italy, Calabria/Basilicata), as well as in *leighebi* and *sbordonii*. This is also the case with *H. mersina* from the Taurus chain in Turkey (Olivier & De Prins, 1989). The absence of the sphragis in *H. turcmenica* is probably due to secondary loss (or simply because of lack of material), but that problem is beyond the scope of the present study.

As a result of our analysis, only three out of Balletto *et al.*'s (1990) 27 characters, when slightly modified and/or formulated differently, were retained as useful for constructing a cladogram of *Parahipparchia*, i. e. B15 [= 9], B21 [= 13] and B27 [= 16]. Nevertheless, our preliminary results agree with those presented by these authors (on p. 185, fig. 3) in the following respects :

- *azorina*, "*caldeirensis*" [*occidentalis*] and *miguelensis* form a monophyletic unit (our characters 3, 4, 8, 10, 11 and 14)
- the *H. semele* group also comes out as a monophyletic unit (our characters 15 and 16)
- *H. volgensis*, *H. turcmenica*, *H. christenseni* and *H. pellucida* constitute a monophyletic subunit within the *H. semele* group (our character 9).
- the same subgroup plus *H. mersina* and *H. cretica* makes up a larger monophyletic subunit within the *H. semele* group (our character 13).

Altogether, we found 16 characters of potential use for our purpose, including six wing characters, one relating to the androconial scales,

two to the male genitalia, six to the female genitalia and one to the presence vs. absence of a sphragis in mated females. Out of these characters, only 13 are synapomorphic, while the remaining three are autapomorphies : hence only 12 adult characters appear valuable for a measure of the relative degree of relationship between taxa within *Parahipparchia*, as character 7 is a synapomorphy of the whole subgenus. We expect that, perhaps with the aid of more refined, statistical procedures, some other characters including part of those advanced by Balletto *et al.* (1990), be it in a slightly different formulation, will perhaps become available and useful. In the next section, we discuss the consequences of the results obtained from our character analysis.

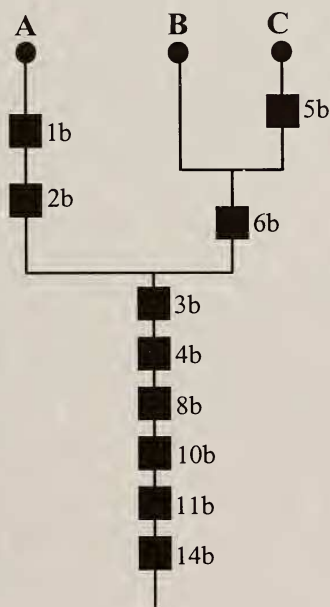


Fig. 32. Cladogram of superspecies *Hipparchia azorina*. A. *H. (azorina) miguellenis* (Le Cerf, 1935); B. *H. (azorina) azorina azorina* (Strecker, 1899); C. *H. (azorina) azorina azorina occidentalis* Bivar de Sousa, 1982. Numbers correspond to apomorphies discussed in section 7.

8. Discussion

8.1. Superspecies *Hipparchia azorina*

The current debate among historical biogeographers whether the present-day distribution patterns of organisms are the result of either vicariance or dispersal, is far from settled (Myers & Giller, 1988). As is often the case with such polemics, time will probably show increasingly that these apparently conflicting views are complementary rather than antagonistic. In the case of the North Macaronesian islands (Azores, Madeira), it seems beyond doubt now that they are of oceanic origin (Mitchell-Thomé, 1982); hence, the current *Hipparchia* species observed there can only have arrived through long-distance dispersal.

The monophyly of superspecies *H. azorina* is well supported (text fig. 32; see also section 7), thus strongly suggesting that the current Azorean populations result from one single colonization event. The ancestor of this superspecies acquired its present synapomorphies either in its source area or, what seems more likely, they developed *in situ*. The common use of one single larval host-plant, if that grass species proves endemic to the Azorean archipelago (we have no data at hand), would lend further support to the latter possibility (it could then be listed as an additional synapomorphy of superspecies *H. azorina*). Which single island was colonized first is a matter of conjecture, but the cladogram on text fig. 32 suggests that *miguelensis* split off first, as it lacks character state 6b that is shared by both *azorina* and *occidentalis* (see also discussion of character 3!): it developed some distinct features of its own (characters 1b and 2b). An initial arrival on the Azores by way of the eastern island group thus seems quite plausible, whereby the present-day absence of any *Hipparchia* on Santa Maria in no way excludes the possibility of its past colonization by the ancestor of superspecies *H. azorina*. Subsequently, the central and western groups were reached from the east, probably first Pico and Faial, whose populations still retain the plesiomorphic character state 5a. Later on, the remainder of the archipelago was reached: the precise sequence of colonization of each island is impossible to reconstruct at present, but there is some evidence that the islands of São Jorge and Terceira — geographically the nearest — were reached first (in São Jorge material, there are sometimes still traces of a sex brand) and that the western group (Flores and Corvo) was the latest to be invaded. The common possession of character state 5b (and the invariably distinct light colouring of the basal and discal area of upperside forewing in the males) in *occidentalis* was probably acquired

first by one single island population of this subspecies, after which it spread to the other islands in a quite recent past. Alternatively, these features were each acquired independently by each single island population of this taxon, a scenario that is less parsimonious and hence more unlikely. The sequence of colonization just outlined correlates rather well with the comparative geomorphological age of the different islands and island groups (Mitchell-Thomé, 1982; Forjaz *in* Vieira & Pintureau, 1991). According to these authors, São Miguel is about 3.5 to 4.5 million years old while Flores has less than 0.6 million years (no data for Corvo). According to Forjaz *in* Vieira & Pintureau (1991), the central group originated between 2.6 (Faial) and 0.6 (Graciosa) million years ago, with about 2.0 million years for São Jorge and Terceira and 1.1 million years for Pico. It would be most rewarding to test this possibility by an independent method and molecular data (e. g. allozymes) seem to offer promising perspectives (cf. Cesaroni *et al.*, 1994). At present, however, we have no further clues at hand: in order to improve our insights into the evolutionary history of superspecies *H. azorina*, we should know which is its sister group or species. Kudrna (1977), Bivar de Sousa (1982a, 1985a) and Balletto *et al.* (1990) have suggested that it is probably one of the phylogenetically oldest taxa of the genus, though they do not present any hard evidence in support of their view. Several authors have suggested a close affinity to the *H. aristaeus* group (Kudrna, 1977; Balletto *et al.*, 1990) or even to *H. maderensis* in particular (Rebel, 1940b; Bernardi, 1961; Meyer, 1993), Bivar de Sousa (1982a) even stating that *miguelensis* is the oldest taxon, probably originating from Madeira from the ancestor of *H. maderensis*. An affinity with *H. maderensis* would seem likely at first sight because of the relative geographical proximity of São Miguel to Madeira and the superficial similarity of both *H. maderensis* and superspecies *H. azorina* (and especially *miguelensis*) in wing pattern (very dark upperside with reduced markings): the latter feature, however, is most probably the result of a common response to the oceanic climate and hence no indication of close phylogenetic relationship. There is indeed no support at all for a sister group relationship between superspecies *H. azorina* and either the *H. aristaeus* group or one of its component species, the relative similarity of these taxa being due to the common possession of symplesiomorphic characters. What seems probable however, is that, within *Parahipparchia*, both superspecies *H. azorina* and the *H. aristaeus* group taxa split off before the common ancestor of the *H. semele* group. As a matter of fact, we cannot decide at present to which other *Parahipparchia* taxon superspecies *H. azorina* is most closely related, nor can we form any possible hypothesis concerning its likely source area.

8.2. The *Hipparchia aristaetus* group

As already stated (section 5), the *H. aristaetus* group could very well be a paraphyletic assemblage : a thorough search for synapomorphies in *Parahipparchia* (section 7) did not produce one single character that could be positively interpreted as a synapomorphy of this species group. The geographic distribution of each of its four composing nominal taxa suggests an ancient, relict pattern. The directional argument of vicariance, as used in the methodology of phylogenetic systematics, cannot be applied, as this presupposes the monophyly of the group in question. Whether we like it or not, in absence of any positive evidence for the monophyly of this group, it is senseless to discuss this problem further until more data become available.

8.3. Priorities for future study

While it is true that we could not find any evidence in favour of the monophyly of the *H. aristaetus* group, it is equally true that there is no evidence at all against it. We feel that the most promising areas for future research would be a thorough investigation of the comparative morphology of the early (and adult) stages of all *Parahipparchia* and *Hipparchia s. str.* taxa in order to find additional synapomorphies that would corroborate (or perhaps, contradict) our present results and provide solutions to some at present unresolved problems encountered with the phylogenetic reconstruction of *Parahipparchia* (i. e. ranking of superspecies *H. azorina*, ranking and phylogeny of the taxa currently placed in the *H. aristaetus* group, ranking and phylogeny of *H. semele* + *H. leighebi* + *H. sbordonii*, resolution of the phylogeny of the individual taxa within the complex *H. volgensis* + *H. turcmenica* + *H. christenseni* + *H. pellucida*) and, in parallel, a comprehensive study of molecular and allozyme data as an independent test of the phylogeny based on the morphological data set as well as a means of estimating the possible divergence time of the taxa under consideration (the study by Cesaroni *et al.*, 1994 is a first interesting endeavour in this field). We hope that the present study will have contributed to setting a framework for further study on these and related topics, and that it may be an impetus for it.

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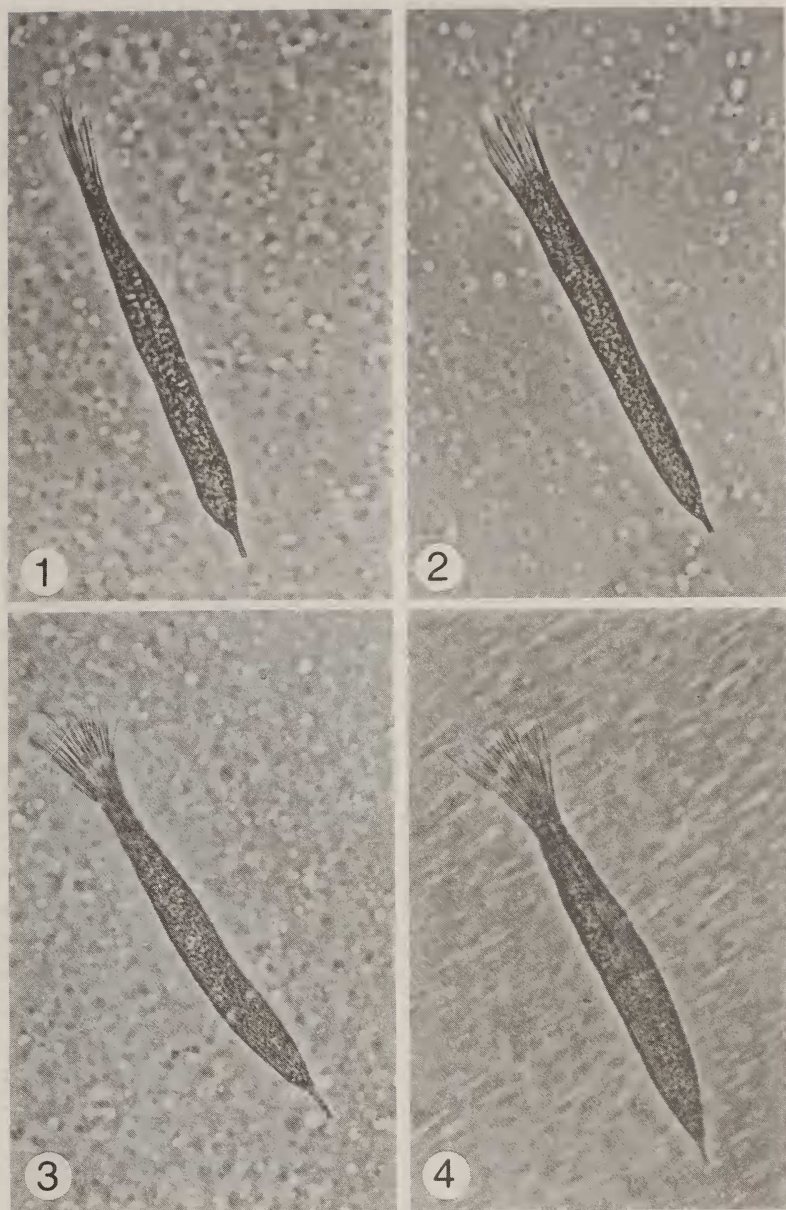


Plate 5. *Hipparchia (azorina) azorina azorina* (Strecker, 1899) : androconial scales.
1-2. Portugal, Azores, Pico, C. do Teicho (850-920 m), 17.VIII.1981, leg. J. Demange,
in coll. VLCA.
3-4. Portugal, Azores, Faial, Caldeira/Cabeço Gordo (900 m), 12.VIII.1990, leg. M.
Meyer, in coll. VLCA.

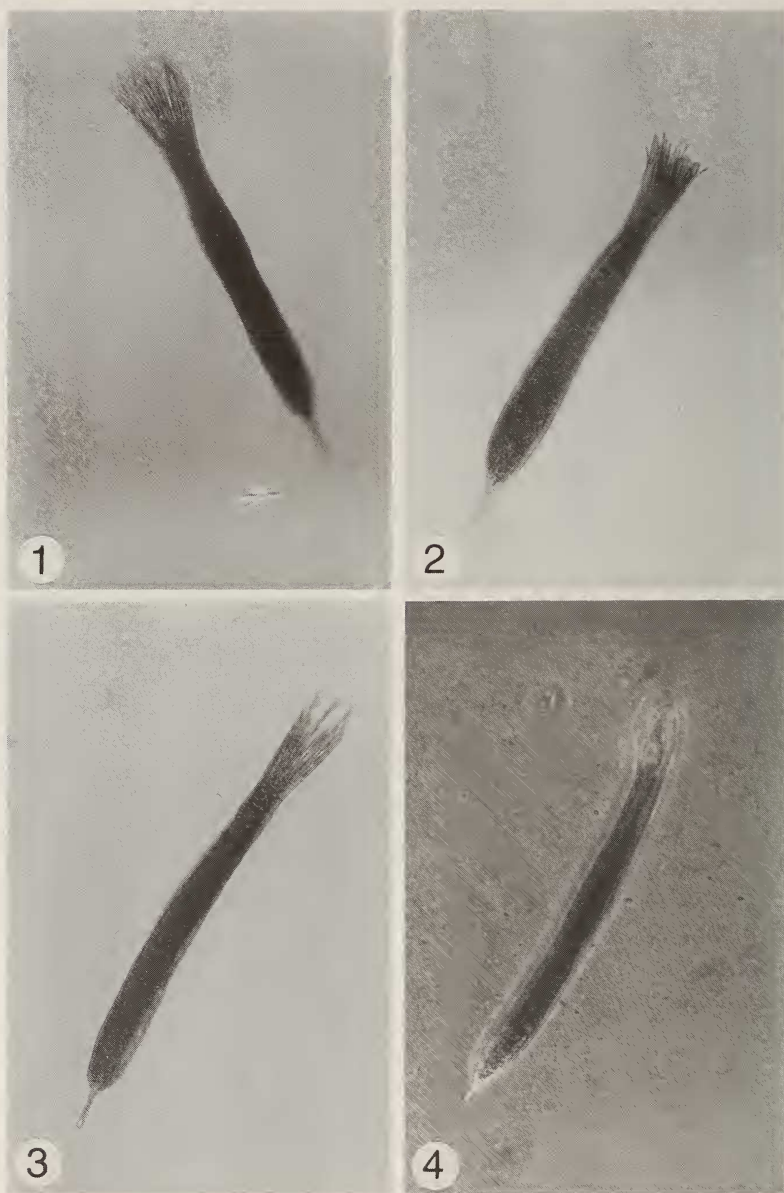


Plate 6. *Hipparchia (azorina) azorina occidentalis* Bivar de Sousa, 1982 : androconial scales.

1-2. Portugal, Azores, São Jorge, Serra do Topo, Pedra Vermelha (800 m), 17.VIII.1990, leg. M. Meyer, in coll. VLCA.

3. Portugal, Azores, Terceira, Serra de Santa Barbara (1000 m), 19.VIII.1990, leg. M. Meyer, in coll. VLCA.

4. Portugal, Azores, Terceira, Serra de Santa Barbara (1000 m), 17.VII.1994, leg. H. Henderickx, in coll. VLCA.

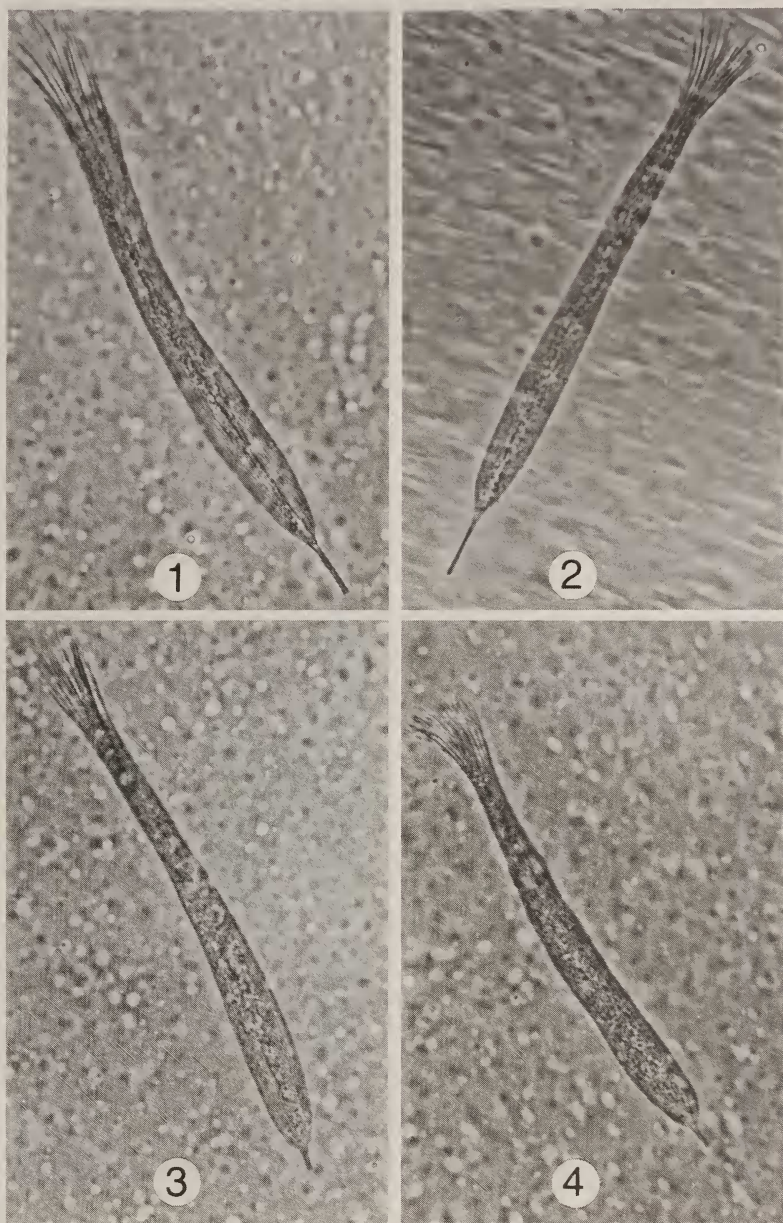


Plate 7. *Hipparchia (azorina) miguelensis* (Le Cerf, 1935) : androconial scales.
1-4. Portugal, Azores, São Miguel, Serra de Agua de Pau (900 m), 24.VII.1994, leg.
H. Henderickx, in coll. VLCA.

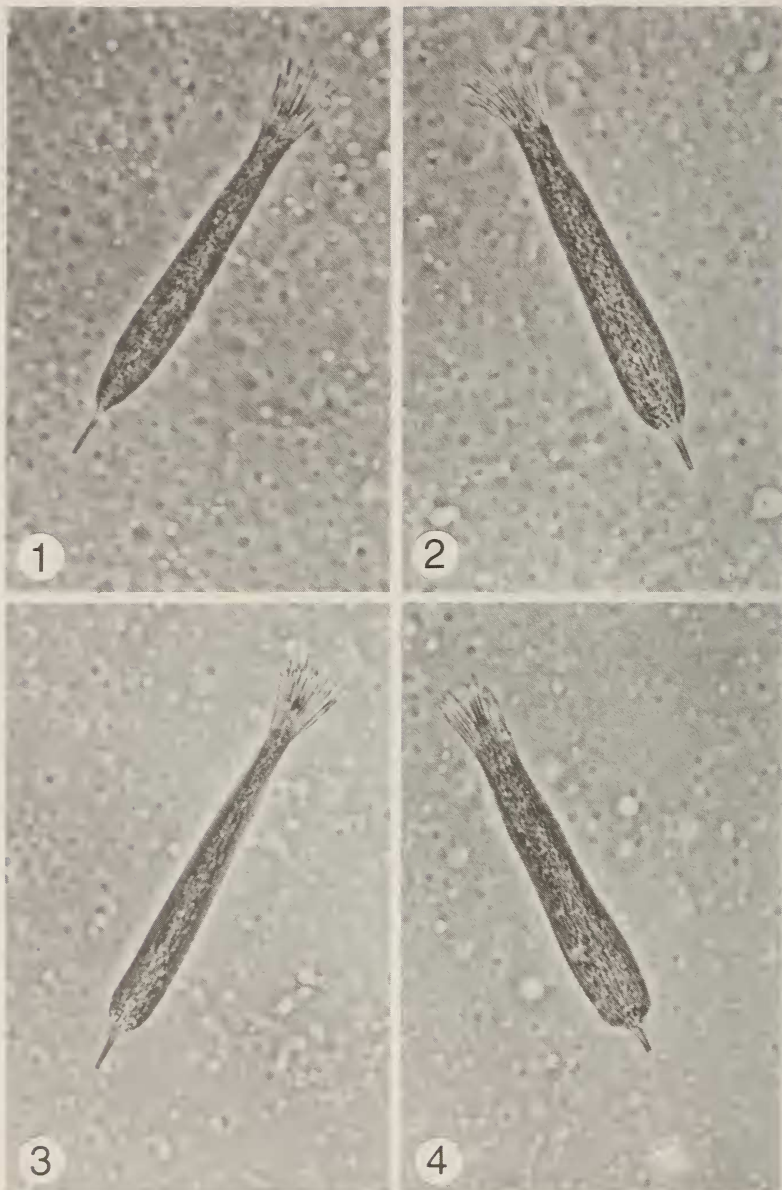


Plate 8. *Hipparchia maderensis* (Baker, 1891) : androconial scales.

1. Portugal, Madeira, 2 km SW. Poiso (1350 m), 29.VII.1993, leg. A. Olivier, in coll. VLCA.

2. as 1, but 25.VII.1993.

3. Portugal, Madeira, Eira do Serrado (1000–1050 m), 24.VII.1993, leg. A. Olivier, in coll. VLCA.

4. Portugal, Madeira, Curral das Freiras (600–700 m), 24.VII.1993, leg. A. Olivier, in coll. VLCA.

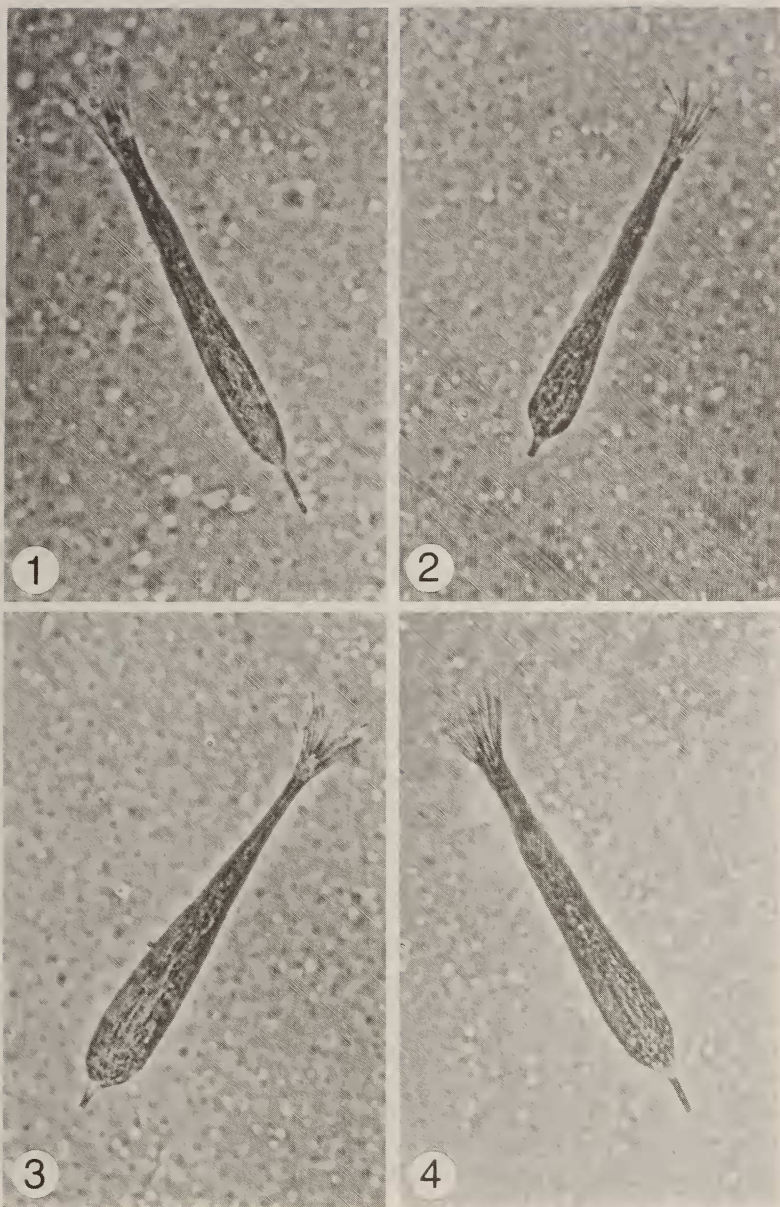


Plate 9. *Hipparchia algirica* (Oberthür, 1876) : androconial scales.
1. Morocco, Middle Atlas, Ifrane (1650 m), 24.VI.1994, leg. A. Olivier, in coll. VLCA.
2. Morocco, Middle Atlas, Tizi-n-Tretten (1950 m), 27.VI.1994, leg. A. Olivier, in coll. VLCA.
3. as 2, but 22.VI.1994.
4. Morocco, Middle Atlas, Ras-el-Ma-Cèdre Gouraud (1600-1700 m), 25.VI.1994, leg. A. Olivier, in coll. VLCA.

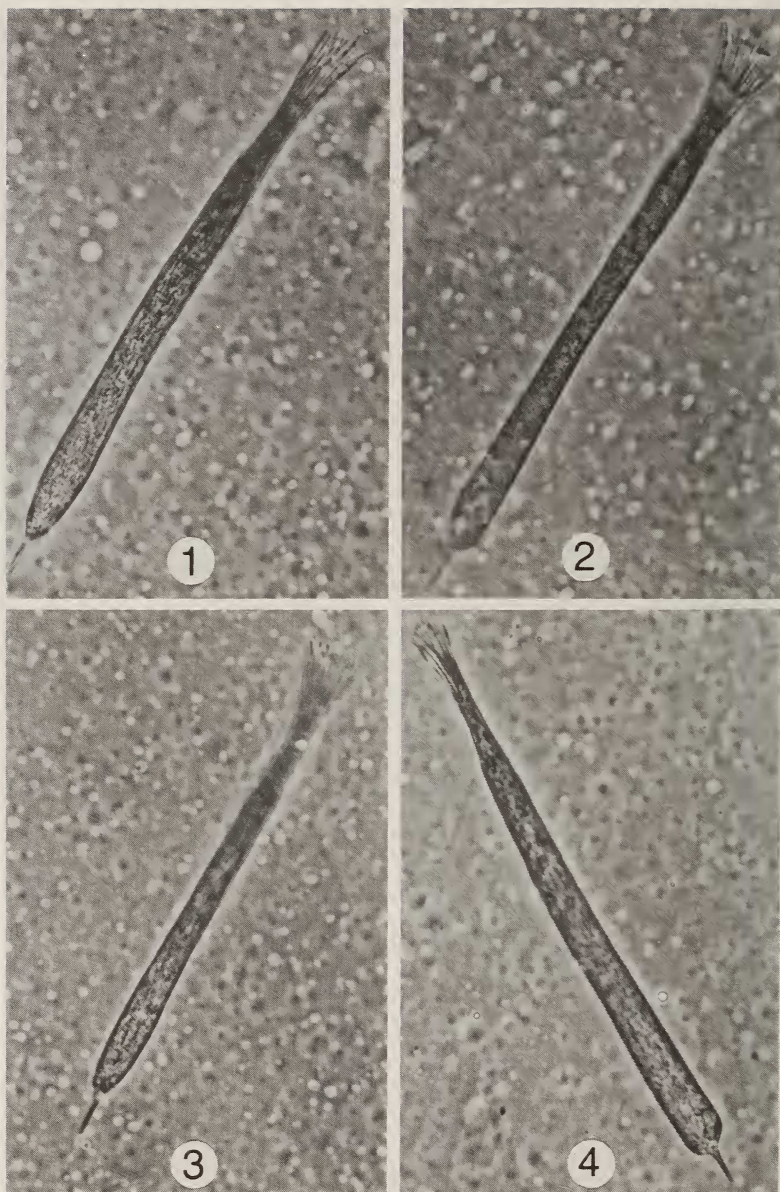


Plate 10. *Hipparchia aristaeus* (Bonelli, 1826) : androconial scales.

1. Italy, Sardinia, Prov. Nuoro, Monti del Gennargentu, 4 km S. Fonni (1000 m), 22.VII.1992, leg. A. Olivier, in coll. VLCA.

2. as 1, but 23.VII.1992.

3. France, Corsica, Haute-Corse, Calvi, 13/27.VII.1971, leg. Fam. van Oorschot & Fam. Coene, in coll. VLCA.

4. Italy, Elba, Mt. Le Calanche (approx. 800 m), 9.VII.1988, leg. C. Warnotte, in coll. VLCA.

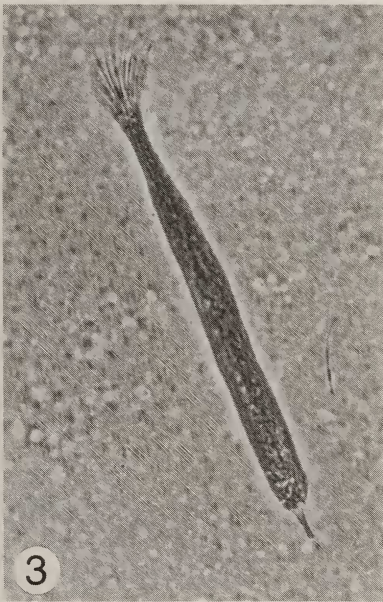
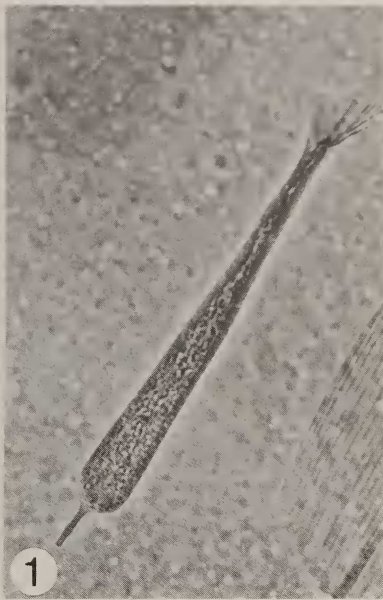


Plate 11. *Hipparchia senthes* (Fruhstorfer, 1908) : androconial scales.

1. Turkey, Prov. Adana, S. Tekir (900 m), 8/10.VIII.1984, leg. B. van Oorschot, in coll. VLCA.

2. Turkey, Prov. Konya, Sultandağları, Akşehir (1100 m), 13/20.VII.1981, leg. H. & Th. van Oorschot & H. van den Brink, in coll. VLCA.

3. Turkey, Prov. Muğla, 60 km NE. Fethiye (1050 m), 8.VII.1981, leg. H. & Th. van Oorschot & H. van den Brink, in coll. VLCA.

4. Turkey, Prov. Muğla, W. side Ak Dağ, Arsada (1000 m), 5.VII.1981, leg. H. & Th. van Oorschot & H. van den Brink, in coll. VLCA.

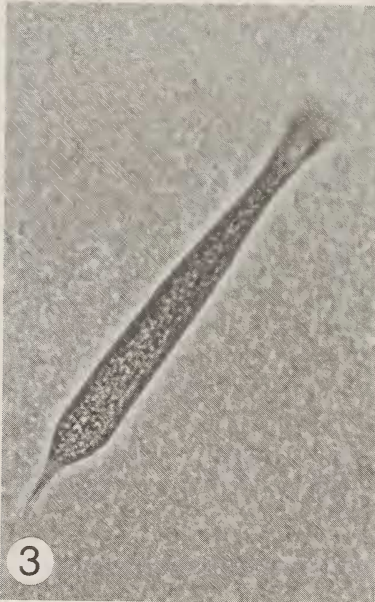
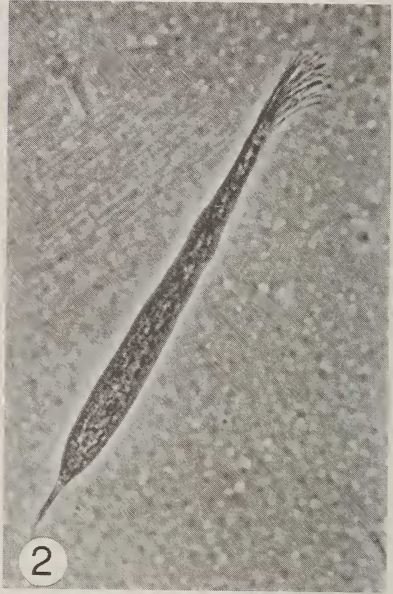
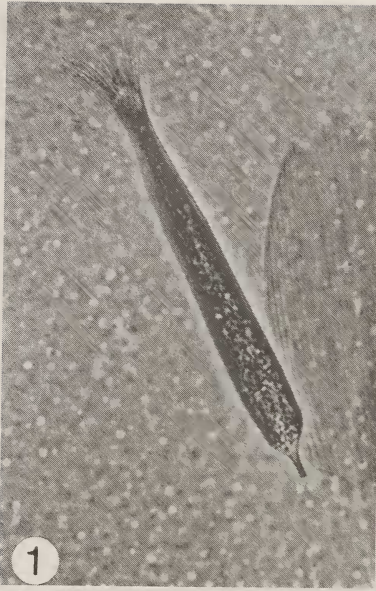


Plate 12. *Hipparchia senthes* (Fruhstorfer, 1908) : androconial scales.

1. Greece, Eastern Aegean islands, Kós, Óros Díkeos (750–846 m), 4.VI.1992, leg. A. Olivier, in coll. VLCA.

2. Greece, Eastern Aegean islands, Sámos, Óros Kerketeús (950–1200 m), 20.VII.1989, leg. A. Olivier, in coll. VLCA.

3. Greece, Eastern Aegean islands, Híos, Néa Moní (500 m), 25.V.1986, leg. A. Olivier, in coll. VLCA.

4. Greece, Eastern Aegean islands, Híos, Nagós (50 m), 7.VI.1987, leg. A. Olivier, in coll. VLCA.

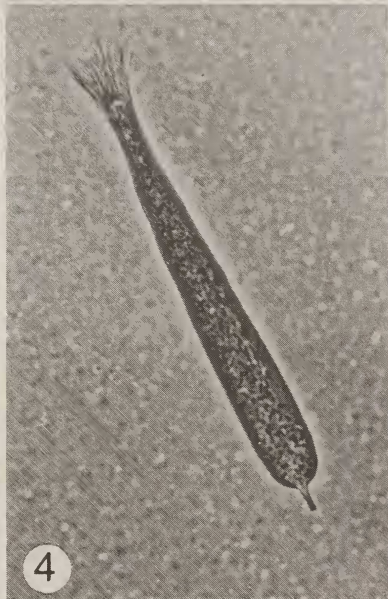


Plate 13. *Hipparchia senthes* (Fruhstorfer, 1908) : androconial scales.

1. Greece, Kikládés, Santoríni, near Episkopi (180–250 m), 19/21.VI.1993, leg. J.G. Coutsis, in coll. VLCA.

2. Greece, Makedonía, Dráma, Óros Falakró (700 m), 20.VII.1982, leg. J. Dils, in coll. VLCA.

3. Greece, Stereá Eláda, Fókida, Delfí (550 m), 20.V.1985, leg. A. Olivier, in coll. VLCA.

4. Greece, Pelopónissos, Lakonía, Óros Taígetos (1600 m), 15.VII.1983, leg. D. van der Poorten, in coll. VLCA.

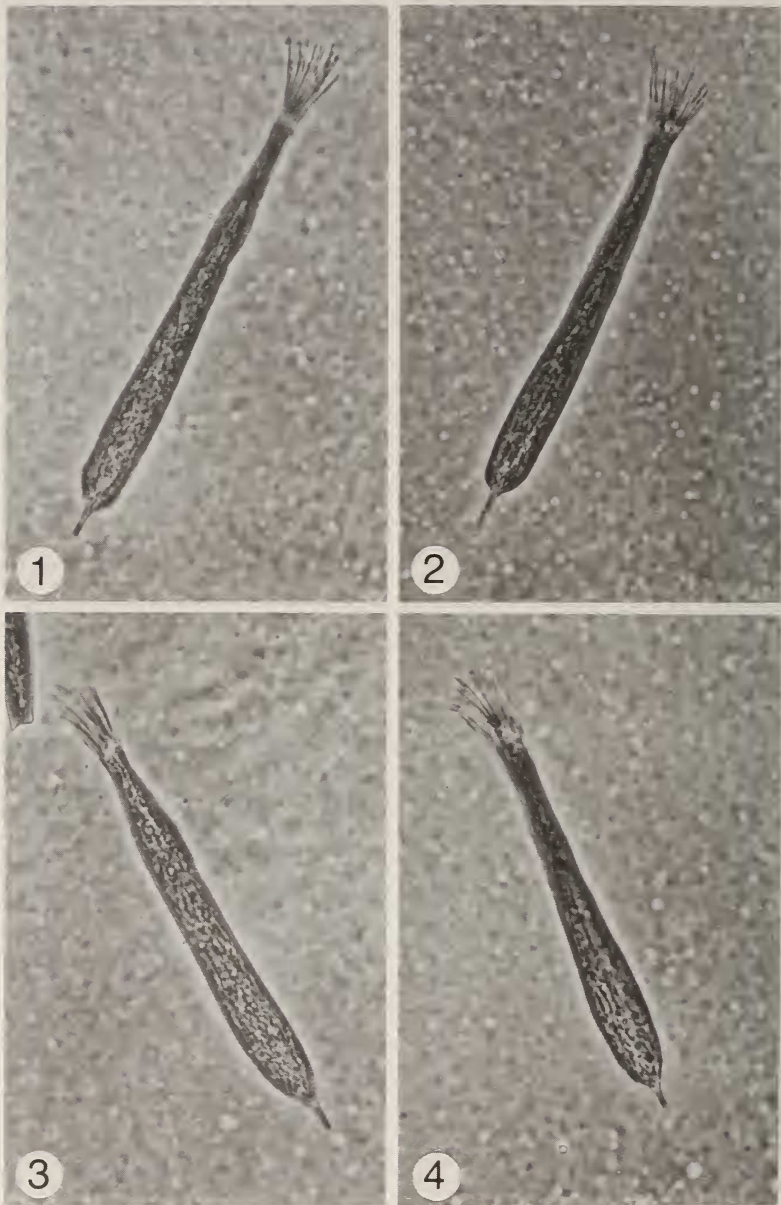


Plate 14. *Hipparchia senthes* (Fruhstorfer, 1908) : androconial scales.

1-2. Italy, Sicily, Prov. Palermo, Monti Le Madonie, Castelbuono (500 m), 15.VII.1991, leg. A. Olivier, in coll. VLCA.

3. Italy, Sicily, Prov. Palermo, Monti Le Madonie, 3 km N. Petralia Sottana (900 m), 16.VII.1991, leg. A. Olivier, in coll. VLCA.

4. Italy, Sicily, Prov. Palermo, Monti Le Madonie, Cozzo Pomieri, 7 km NW. Petralia Sottana (1150-1300 m), 17.VII.1991, leg. A. Olivier, in coll. VLCA.

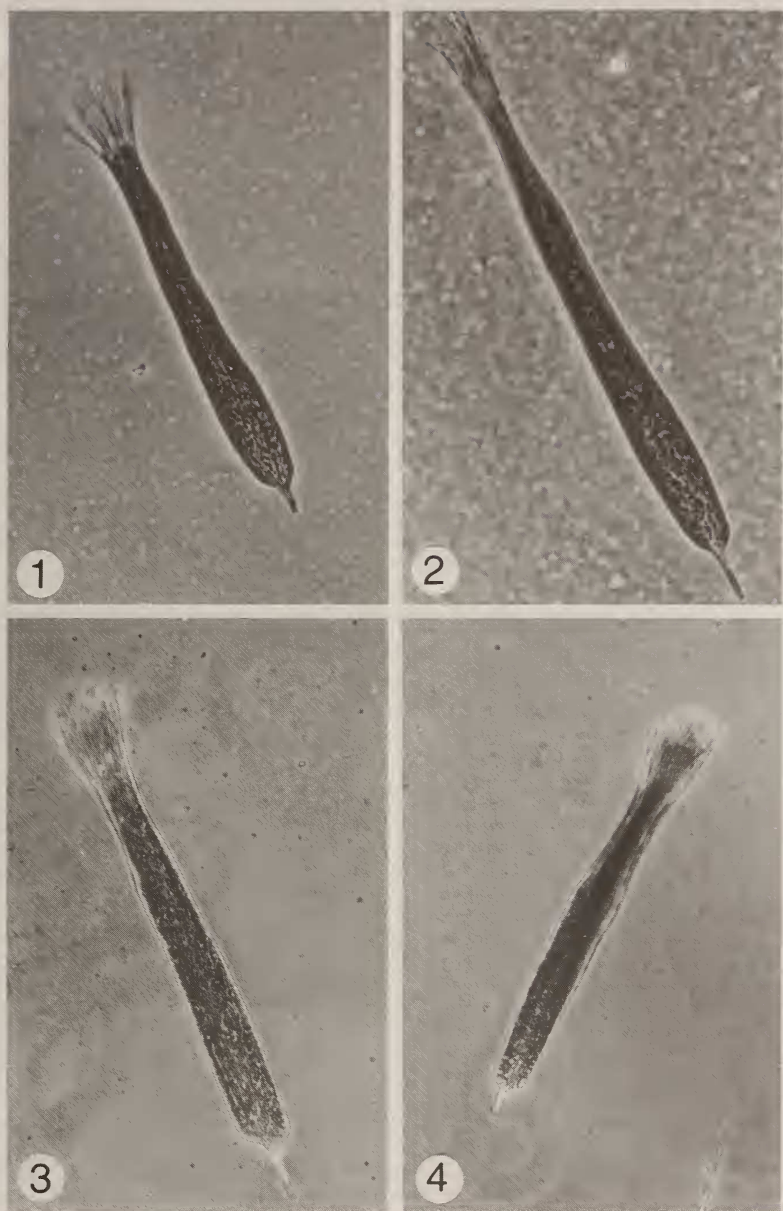


Plate 15. *Hipparchia senthes* (Fruhstorfer, 1908) : androconial scales.

1. Italy, Calabria, Prov. Reggio, Aspromonte, 5-8 km SSE. Gambárie (1600-1700 m), 23.VII.1995, leg. A. Olivier, in coll. VLCA.

2. as 1, but 24.VII.1995.

3. Italy, Calabria, Prov. Cosenza, La Sila, Cerenzia (600-650 m), 28.VII.1995, leg. A. Olivier, in coll. VLCA.

4. as 3, but 26.VII.1995.

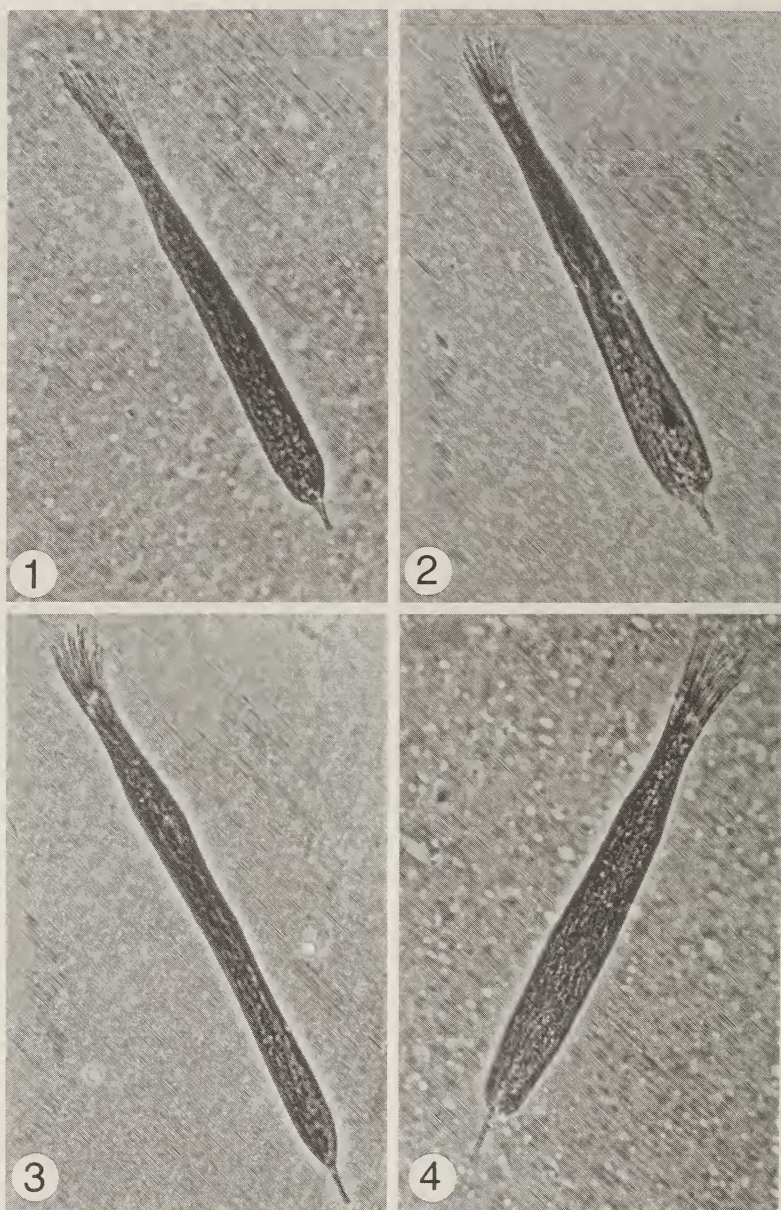


Plate 16. *Hipparchia senthes* (Fruhstorfer, 1908) : androconial scales.
1-3. Italy, Campania, Prov. Nápoli, Monte Faito (1000-1100 m), 23.VII.1991, leg.
A. Olivier, in coll. VLCA.
4. Italy, Campania, Prov. Nápoli, Ísola d'Íschia, Fontana (400 m), 8.VII.1991, leg.
A. Olivier, in coll. VLCA.

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Glossary of terms used in studies on phylogenetic systematics, as mentioned partly in the present study

apomorphy : of a homologous pair of characters, the apomorphic character [or apomorphy] is the character evolved directly from its preexisting homologue (synonyms : apomorphous character, derived character, advanced character and specialized character) (Wiley, 1981 : 122).

autapomorphy : a character evolved from its plesiomorphic homologue in a single species (Wiley, 1981 : 123). Hennig (1979 : 90) called autapomorphous characters “the apomorphous features characteristic for a particular monophyletic group (present only in it) that can be ignored in discussing its relations to other groups”, while Ax (1987 : 3) defined it as “each evolutionary novelty of the stem species”. In the present study, we consequently apply this term in Wiley’s sense, to denote an apomorphy restricted to one single species. According to the definitions of Hennig (1979) and Ax (1987), the teeth on the penis in superspecies *H. azorina* would have been an autapomorphy of this taxon. To the contrary, we call it a synapomorphy of this superspecies, because it is shared by its two component sister species, *H. (azorina) azorina* and *H. (azorina) miguelensis*, i. e. it gives us information on their supposed monophyly and degree of relationship. It is true that this character does not give us any information on the degree of relationship of superspecies *H. azorina* with any other *Parahipparchia* taxon. Autapomorphies are useful to characterize a species (as a diagnostic feature), but useless for determining its degree of relationship with other species or supraspecific taxa.

cladogram : a branching diagram of entities where the branching is based on the inferred historical connections between the entities as evidenced by synapomorphies. That is, a cladogram is a phylogenetic or historical dendrogram.

convergence : development of similar characters from different pre-existing characters (Wiley, 1981 : 12). Compare to homoplasy and parallelism.

correlation of transformation series (directional argument of) : if in a monophyletic group two or more phenoclines occur in the same species, the direction of change is identical in these transformation series (de Jong, 1980 : 14).

dendrogram : a branching diagram containing entities linked by some criterion (Wiley, 1981 : 97).

differentiation and complexity (directional argument of) : in a monophyletic group the character states that show the highest degree of differentiation or complexity are the apomorphous states (de Jong, 1980 : 19).

homology : a character of two or more taxa is homologous if this character is found in the common ancestor of these taxa, or, two characters (or

a linear sequence of characters) are homologues if one is directly (or sequentially) derived from the other(s) (Wiley, 1981 : 121–122).

homoplasy (nonhomology) : a character found in two or more species is homoplasous (nonhomologous) if the common ancestor of these species did not have the character in question, or if one character was not the precursor of the other (Wiley, 1981 : 122). Compare to convergence and parallelism.

monophyletic group : a group of species that includes an ancestral species (known or hypothesized) and all of its descendants (Wiley, 1981 : 76, 84). Characterization (cf. Hennig, 1979) : a group based on synapomorphous similarity.

monophyly : of a species group when its members, without exception, descend from a single stem species shared by them alone (Ax, 1987 : 21).

outgroup : an outgroup is a species or higher monophyletic taxon that is examined in the course of a phylogenetic study to determine which of two homologous characters may be inferred to be apomorphic. One or several outgroups may be examined for each decision. The most critical outgroup comparisons involve the sister group of the taxon studied (Wiley, 1981 : 7).

outgroup occurrence (directional argument of), often termed “outgroup comparison” : if a character occurs in more than one state in a monophyletic group, the state that occurs also outside the group is likely to be the plesiomorphic state (de Jong, 1980 : 12).

parallelism (or parallel development) : the independent development of similar characters from the same plesiomorphic character (Wiley, 1981 : 12). Compare to convergence and homoplasy.

paraphyletic group : a group [of species] that includes a common ancestor [an ancestral species (known or hypothesized)] and some but not all of its descendants (Wiley, 1981 : 84). Characterization (cf. Hennig, 1979) : a group based on symplesiomorphous characteristics.

plesiomorphy : of a pair of homologues, the plesiomorphic character [or plesiomorphy] is the character that arose earlier in time and gave rise to the later, apomorphic character (synonyms : plesiomorphous character, primitive character, ancestral character and generalized character) (Wiley, 1981 : 122).

polyphyletic group : a group [of species] in which the most recent common ancestor [an ancestral species (known or hypothesized)] is assigned to some other group and not to the group itself (Wiley, 1981 : 84). Characterization (cf. Hennig, 1979) : a group based on convergent similarity.

reversibility (reversal of character state) : a character that reverts to its original condition (Hennig, 1979 : 93). A reversal to the structurally plesiomorphic condition in one particular species should be considered as an autapomorphy of that species (e.g. the neomorphic androconium in *H. mersina*, cf. section 1 : Introduction).

sister groups : species groups that arose from the stem species of a monophyletic group by one and the same splitting process (Hennig, 1979 : 139).

sister species : two species that arose from the stem species shared only by them by one and the same splitting process (our definition). For this and the foregoing case, Ax (1987 : 36) coined the term adelphotaxon, which he defined as follows : “Adelphotaxa are evolutionary species, or monophyletic species groups, of the first degree of phylogenetic relationship. They arise by the dichotomous splitting of a stem species common to them alone”. As this term has not been widely used (or perhaps not at all) in literature on Lepidoptera phylogeny, we prefer to mention the terms “sister groups” and “sister species”.

specialization (directional argument of) : a character state is considered apomorphous, if it restricts the niche of the organism. Niche restriction means restriction to a particular mode of life or to a particular environmental factor (de Jong, 1980 : 16).

symplesiomorphy : a shared plesiomorphy [by two or more taxa] (Wiley, 1981 : 123). Ax (1987 : 53) gives a more complete and explicit definition : “An agreement between evolutionary species or monophyletic species groups in a feature which did not arise in their common stem lineage but was taken over from stem species that were even more remote”.

synapomorphy : a homologous character found in two or more taxa that is hypothesized to have arisen in the ancestral species of these taxa and in no earlier ancestor (Wiley, 1981 : 123).

vicariance (directional argument of) : if in a monophyletic group two species are vicarying, these species are more closely related to each other than to any other species, and character states restricted to them are considered apomorphous (de Jong, 1980 : 17).